

doideae encompasses ca. 190 genera (for more details see: "Tribal disposition of Periplocoideae and Asclepiadoideae genera," <<http://www.uni-bayreuth.de/departments/planta2/>>) and more than 2500 species. Relationships within this subfamily are most accurately represented by four tribes: the basal Fockeeae, the Marsdenieae, the Ceropogieae Orb. (this name replaces the up to recently used but younger name Stapelieae Decne.; cf. Endress & Bruyns, 2000), and the Asclepiadeae, which probably is the most advanced. The latter is subdivided into seven subtribes (sensu Liede, 1997, 2001 this volume).

Many studies have demonstrated the taxonomic value of chromosomal information in the plant kingdom in general (Stebbins, 1971; Lewis, 1980). In Asclepiadoideae, however, due to the dominance of  $2n = 22$  and a "small" chromosome size, chromosomal data have been little used. Only rarely has karyology, in particular polypoidy, been utilized to support taxonomic conclusions or phylogenetic considerations (Meve, 1995a, 1997a). The study presented here is the result of a long-term project, which was initiated by the late G. Reese (Kiel), with chromosome counts for stapeliads (Reese, 1971; Reese & Kressel, 1967) and continued by us. A summary of the previous literature and a first overview were given by Albers (1983), and many of the further counts have been published in Albers (1974, 1975, 1976, 1977, 1981), Albers and Delfs (1983), Albers and Austmann (1987), and Albers et al. (1988, 1990). In the last 20 years we have emphasized karyotype length investigations in addition to the mere chromosome counts, and with the standard use of well-documented voucher material. We expanded the study to all tribes of the Asclepiadoideae (cf. Albers, 1983; Albers et al., 1993; Meve, 1999), as well as to Periplocoideae and Secamonoideae (Appendix 1). In addition, research included measurements of the DNA content (Huesmann, 1993).

## MATERIAL AND METHODS

### MATERIALS

The data gathered and used in this paper regarding Periplocoideae, Secamonoideae, and Asclepiadoideae are based mainly on our own investigations. Appendix 1 summarizes our recent findings and includes two types of data: first chromosome counts for taxa, which are unmarked, and counts confirming previous chromosome numbers, which are preceded by a hatch symbol (#). Where the same chromosome number was counted for different geographic regions, sometimes two different

vouchers of a single taxon are given here. In addition, vouchers for chromosome measurements that are based on plants with already published chromosome numbers are included in Appendix 1. This material is marked by an asterisk (\*). For the different calculations, we considered literature data as far as possible, except for information that was either unreliable or doubtful (e.g., for invalid and dubious taxa, presumably wrong counts, etc.). Chromosome numbers published without voucher provenance have been excluded as well, since the chance of including numbers being attributed to incorrectly determined plants increases considerably using undocumented material.

Information on Apocynoideae and Rauvolfioideae is mainly based on Van der Laan and Arends (1985). Information on Apocynaceae s.l. is supplemented by data extracted from Darlington and Wylie (1955), Fedorov (1974), and various volumes of the *Index to Plant Chromosome Numbers* edited by Ornduff (1967), Moore (1973, 1974, 1977), Goldblatt (1981, 1984, 1985, 1988), and Goldblatt and Johnson (1990, 1991, 1994, 1996, 1998).

### METHODS

Chromosome numbers and chromosome sizes were established from adventitious root tip squash preparations. Ten mitotic metaphase plates from different root tips of each sample were investigated, though ten plates were not available in ca. one third of the samples due to the lack of actively growing root tips. The root tips were prepared as follows: pre-treatment in 0.002 M hydroxyquinoline for 4 hr. at 20°C (Tjio & Levan, 1950); fixation in Carnoy's solution for 24 hr. at 20°C; staining in carmine for 24 hr. at 60°C (Snow, 1963). For cytological investigation a Leitz Orthoplan microscope was used. The total lengths of all chromosomes in the genome were measured on maximally contracted chromosomes on the basis of camera lucida pencil drawings. Control (digital) measurements of the karyotype length were done by using the Leitz Orthoplan microscope in connection with a Leica Quantiment 500 (software QWIN). Measurements of the mean value, standard deviation, and error were part of the Leica program.

For fixations of Feulgen cytophotometric measurements of relative 2C DNA content Carnoy's solution was used (24 hr., 4°C) after pretreatment with 0.002M hydroxyquinoline for 4 hr.; ten fixed root tips from each taxon were hydrolyzed in 5M HCl for 80 min. at 20°C, washed in distilled water for 10 min., and stained in Feulgen reagent for 80 min. at room temperature. The washed root tips were



Table 1. Number and distribution of karyologically known species, subspecies, and varieties in Periplocoideae, Secamonoideae, and Asclepiadoideae (number of karyologically known genera in parentheses following the tribal names).

Chromosome number	PERIPLOCO-IDEAE	SECAMONO-IDEAE	ASCLEPIADOIDEAE			
	— (13)	Secamoneae (1)	Fockeeae (2)	Marsdenieae (7)	Ceropegieae (37)	Asclepiadeae (41)
$2n = 18$						3
$2n = 20$						15
$2n = 22$	27	3	6	29	464	134
$2n = 24$					1	2
$2n = 26$						1
$2n = 28$						1
$2n = 40$						1
$2n = 44$	4	1			36	4
$2n = 66$					5	1
$2n = \text{ca. } 132$					1	
$2n = \text{ca. } 154$						1

incubated in 45% acetic acid for 10 min. Then only the dark-stained tips were squashed and the telophases (2C DNA content) were studied with the aid of a Zeiss scanning microscope photometer (SMP 05) using the two wavelength method published by Ornstein (1952) and Patau (1952), and the wavelengths  $\lambda \text{ max.} = 575 \text{ nm}$  and  $\lambda/2 = 510 \text{ nm}$  as published by Greilhuber (1986). The DNA values were obtained on the basis of optical density. This was converted to pg according to Patau (1952). *Allium cepa* (2C DNA content = 33.5 pg [Bennett & Smith, 1976]) was taken as standard.

## RESULTS

### CHROMOSOME NUMBERS

Karyological information for 672 species, representing ca. 24%, of the three subfamilies Asclepiadoideae, Periplocoideae, and Secamonoideae in 101 genera, representing ca. 44%, and belonging to 740 taxa altogether is summarized in Table 1. The chromosome numbers of 299 taxa are new to science and appear with locality data and vouchers in the compilation of Appendix 1 (unmarked), together with new counts confirming or completing earlier counts (preceded by #). For all counts, also including previously published chromosome numbers of both our and foreign counts, consult the expanded version of Appendix 1 under <<http://www.uni-muenster.de/Biologie/botanik/AgAlbers.htm>> or <<http://www.uni-bayreuth.de/departments/planta2/>>.

The basic chromosome number  $x = 11$  is by far the most predominant number in Asclepiadoideae, Periplocoideae, and Secamonoideae (Table 1; Fig. 2); only ca. 3.5% of the studied species and taxa

deviate from this. Among the deviant base numbers  $x = 10$  (Fig. 3C) is the most frequent (ca. 2.5% of the studied species), followed by  $x = 9$  (ca. 0.5% of the studied species), and the sporadic increasing deviates  $x = 12, 13,$  and  $14$  (Table 1).

In our analysis of the distribution of the basic chromosome number  $x = 11$  in the asclepiad subfamilies, tribes, and subtribes neither the Periplocoideae nor the Secamonoideae contained any deviating numbers (Table 1, Fig. 2, Appendix 1). The same situation is found in the basal Asclepiadoideae tribes Fockeeae and Marsdenieae, the large Ceropegieae, and also in Asclepiadeae in the subtribes Gonolobineae, Asclepiadinae, and Tylophorinae (Table 1, Fig. 2, Appendix 1). All known deviating numbers are scattered among the three Asclepiadeae subtribes Astephaninae, Metastelminae, and Oxypetalinae (Table 1, Appendix 1). No taxonomic subunit above generic level is characterized by a basic number deviating from  $x = 11$ , but single genera like *Microlooma* (Fig. 3C) and *Funastrum*, except *F. crispum* (cf. Appendix 1), share exclusively  $x = 10$  chromosomes (Albers et al., 1993).

### POLYPLOIDY

In the Periplocoideae and Secamonoideae polyploidy occurs only as autopolyploidy, as simple doubling of  $2n = 22$  (Table 1). These genomes with  $2n = 44$  are only known from a few *Raphionacme* species (Fig. 2A), *Periploca viscifformis*, and from one individual of *Secamone parviflora* (Appendix 1).

Approximately 6% of the species in the Asclepiadoideae are polyploids (Table 1). Polyploidy is



known to occur in 17 genera and is based on  $x = 11$ , except for the single determination of  $2n = 40$  for *Tweedia brunonis* (Asclepiadeae, Oxypetalinae, Appendix 1). Some 85% of these polyploids are tetraploid ( $2n = 44$ ) and 12% are hexaploid ( $2n = 66$ ). The remaining instances of polyploidy include dodecaploidy ( $2n = 132$ ) in the stapeliad *Caralluma burchardii* subsp. *burchardii* (Ceropegieae) (Meve, 1995a) and decatetraploidy in the twiner *Tylophora anomala* N. E. Br. (Asclepiadeae, Tylophorinae) (Meve, 1999). The latter taxon also includes the highest number ever found,  $2n = 154$ , in an isolated cytotype on Mt. Cameroon, whereas the frequent East African representative of this species is hexaploid with  $2n = 66$  (Meve, 1999). The majority of polyploids are present in the tribe Ceropegieae, where 9.3% of the species (8.3% of the taxa) were found to be polyploid (Table 1, Fig. 3B). Stem-succulent stapeliad genera like *Duvalia*, *Orbea*, and *Stapelia* have especially high percentages of polyploid taxa (cf. Albers & Meve, 1991). The genus *Duvalia* in southern Africa, in particular, is a classic example of a polyploid complex including several tetraploids and two hexaploids, and contributes considerably to the understanding of phylogeny and biogeography of *Duvalia* and the African stapeliads in general since polyploidy is a uni-directional event (Meve, 1997a).

Intraspecific polyploidy is comparatively rare in the groups investigated. We did not find it in Periplocoideae, and only once in Secamonoideae (*Secamone parviflora*, Appendix 1). In Asclepiadoideae, especially Ceropegieae, it is less rare, but can be restricted to individuals (cf. *Huernia keniensis*, Appendix 1). Also, mixoploid individuals occur with single sections of the root tip meristem being polyploid instead of diploid (e.g., *Caralluma adscendens* var. *gracilis*: Fig. 3B, Appendix 1; cf. also Albers & Meve, 1991). In some cases the different levels characterize infraspecific taxa, e.g., in *Caralluma burchardii* (Meve, 1995a), *Duvalia sulcata* (Meve, 1997a), *Ceropegia racemosa*, and *Orbeopsis gerstneri* (Appendix 1), and in *Sarcostemma viminalis*, where the subspecies *thunbergii* is a tetraploid (Liede & Meve, 1993) while the other seven subspecies are all diploid (Liede & Meve, 1995; Meve & Liede, 1996; Appendix 1).

#### CHROMOSOME MORPHOLOGY

Chromosomes of the groups under discussion are morphologically rather homogeneous. Chromosomes are typically (sub)metacentric, rarely acrocentric, and their karyograms offer very little variation. One pair of chromosomes per genome

possessing secondary constrictions with satellites is the rule as shown in Figure 2A for *Raphionacme hirsuta*, and in Albers (1983: fig. 2a, p. 797) for *Brachystelma dinteri* Schltr. Heterochromatic regions, which have an affinity for Giemsa C-banding stain are consistently located on both sides of the centromere (Albers, 1983: fig. 2b, c) and are therefore of poor taxonomic value. However, the size of chromosomes varies considerably throughout the subfamilies and tribes studied (Figs. 1 and 2).

Single chromosome length varies from ca. 0.6  $\mu\text{m}$  (sometimes less) to 1.7  $\mu\text{m}$  (in rare cases more than 2.0  $\mu\text{m}$ ) comparing the tribes and subfamilies (Fig. 1). Within a single karyotype the chromosomes are comparatively similar in size. Only rarely were heterogeneous karyotypes found where chromosome sizes varied considerably (e.g., *Microlooma incanum*: min. 0.68—max. 1.12  $\mu\text{m}$ , Fig. 3C; *Heterostemma herberti*: min. 0.8—max. 1.4  $\mu\text{m}$ , Meve, unpublished). In other cases, just one pair of chromosomes is ca. 30% larger than all the remaining, similarly smaller chromosomes (e.g., *Glossonema boveanum*, *Pentarrhinum insipidum*) (Appendix 1). The chromosomes of polyploid taxa are usually smaller than those of diploid ones. This behavior is repeated in infraspecific polyploid units, individuals, or mixoploid tissue.

Some general tendencies at subfamilial, tribal, and subtribal level can be recognized. However, it should be kept in mind that sample sizes vary considerably. This is so because most species are rarely collected at all, are difficult to transplant from the wild, and set seed only sporadically. Only species with succulent stems (stapeliads), tubers (e.g., *Raphionacme*), etc., are well represented in collections, whereas the majority of species in all three subfamilies are lianas or herbaceous vines without storage organs. Therefore, access to living material, especially taxa of the subfamily Periplocoideae and Secamonoideae (but also New World taxa), is restricted, and data concerning their chromosomes are in part rather limited despite all efforts made to obtain as much material as possible. As far as known, the average chromosome length in Periplocoideae differs between various genera. Whereas in *Periploca*, *Petopentia*, and *Stomatostemma* chromosomes are on the average about 1  $\mu\text{m}$  long, those of *Raphionacme*, *Taccazea*, and *Schlechterella* (incl. *Triodoglossum*) are strikingly larger (ca. 1.5  $\mu\text{m}$ ; Fig. 1). The few chromosome sizes known for secamonoid taxa reach on the average 1.25  $\mu\text{m}$  in length. This size is similar to that in some Periplocoideae. On the average, however, secamonoid chromosomes are slightly smaller (Fig. 1).

The large subfamily Asclepiadoideae comprises



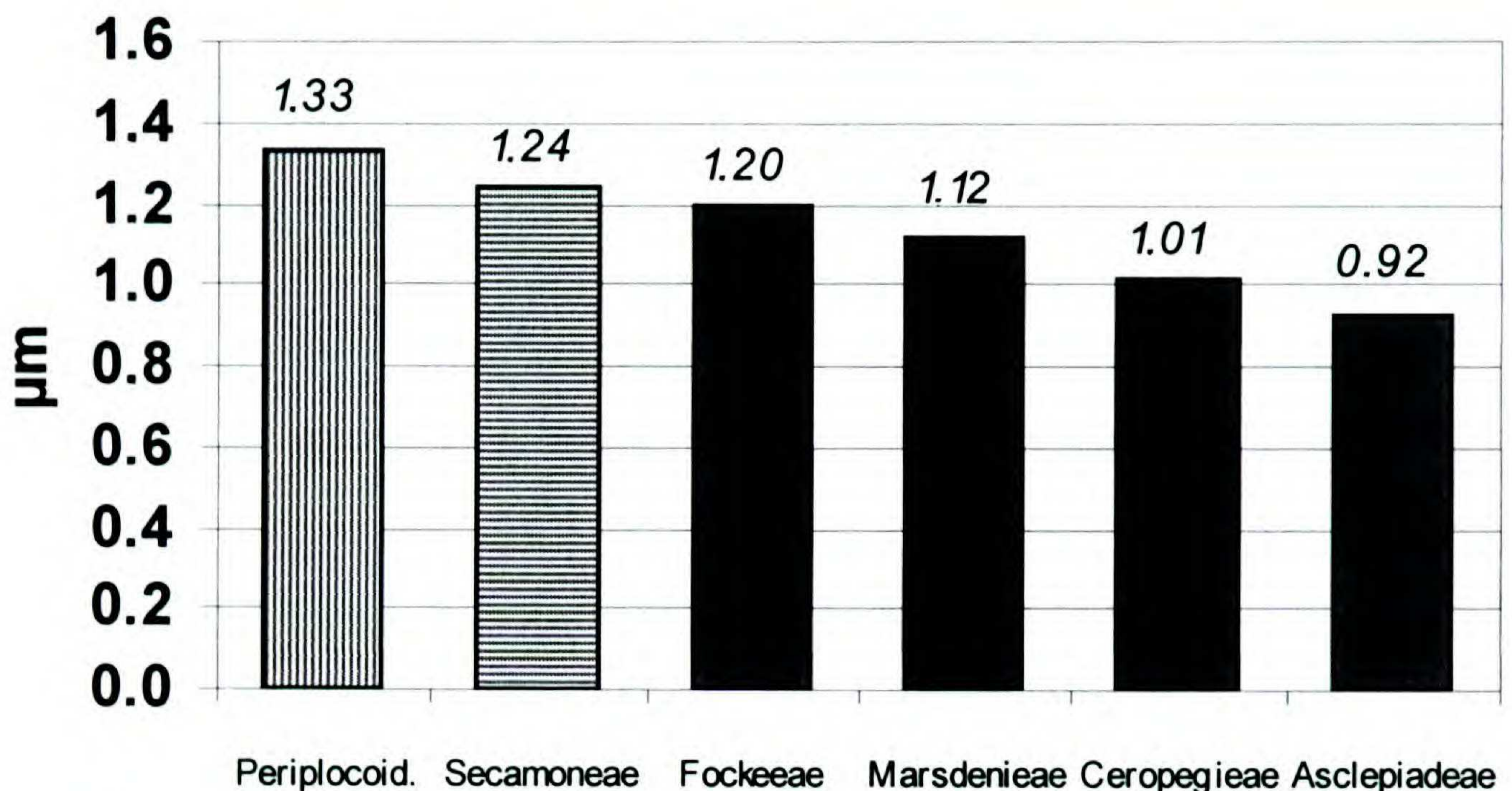


Figure 1. Average chromosome lengths in subfamily Periplocoideae (vertically striped column), Secamonoideae (horizontally striped column), and Asclepiadoideae (gray columns) with the four tribes Fockeeae, Marsdenieae, Ceropegieae, and Asclepiadeae. The ranges are in Periplocoideae:  $\bar{x}$  (min. 1.06  $\mu\text{m}$  [*Stomatostemma*] $\text{---}$ max. 1.61  $\mu\text{m}$  [*Raphionacme*]), number of samples: 12; Secamonoideae:  $\bar{x}$  (min. 1.13  $\mu\text{m}$  $\text{---}$ max. 1.34  $\mu\text{m}$ ), number of samples: 3 *Secamone*; Fockeeae:  $\bar{x}$  (min. 1.15  $\mu\text{m}$  [*Cibirhiza*] $\text{---}$ max. 1.27  $\mu\text{m}$  [*Fockea*]), number of samples: 3; Marsdenieae:  $\bar{x}$  (min. 0.91  $\mu\text{m}$  [*Hoya*] $\text{---}$ max. 1.44  $\mu\text{m}$  [*Telosma*]), number of samples: 17; Ceropegieae:  $\bar{x}$  (min. 0.68  $\mu\text{m}$  [*Duvaliandra*] $\text{---}$ max. 1.72  $\mu\text{m}$  [*Neoschumannia*]), number of samples: 176; Asclepiadeae:  $\bar{x}$  (min. 0.74  $\mu\text{m}$  [*Philibertia*] $\text{---}$ max. 1.15  $\mu\text{m}$  [*Gomphocarpus*]), number of samples: 55.

the four tribes Fockeeae, Marsdenieae, Ceropegieae, and Asclepiadeae. The Gonolobae, which were earlier considered to be a tribe of their own, were transferred by Liede (1997) as subtribe Gonolobinae to the Asclepiadeae. The chromosomes of the Fockeeae have an average length of 1.20  $\mu\text{m}$ , which is not much shorter than in the Secamonoideae (1.24  $\mu\text{m}$ , Fig. 1). The chromosome lengths in the remaining tribes are on average smaller, being 1.12  $\mu\text{m}$  in Marsdenieae, 1.01  $\mu\text{m}$  in Ceropegieae, and 0.92  $\mu\text{m}$  in Asclepiadeae (Fig. 1). The situation in the tribe Marsdenieae is similar to the two groups presented above: parts of the genera *Telosma* and *Marsdenia* have rather large chromosomes (ca. 1.4  $\mu\text{m}$  on the average, but just 1.12  $\mu\text{m}$  in the depicted *Telosma accedens*, Fig. 2D), while all other marsdeniads investigated have smaller chromosomes around 1  $\mu\text{m}$ . The best studied group is the tribe Ceropegieae, where the stem-succulent representatives such as *Caralluma*, *Huernia*, *Orbea*, *Stapelia*, etc., the “stapeliads,” represent the main stock of species (ca. 350), followed by *Ceropegia* (180) and *Brachystelma* (ca. 100 species). Almost 90% of the stapeliad species and infraspecific taxa are karyologically known, the best characterized group in the family. The smaller genera such as *Hoodia*, *Stapelianthus*, or *Tridentea* are usually rather homogeneous as to chromosome

size, but as the size of the genera increases, variation proportionally increases in some genera. For example, in the large genus *Ceropegia*, the average chromosome length varies between 0.8  $\mu\text{m}$  (*C. occidentalis*) and ca. 1.5  $\mu\text{m}$  (*C. rupicola*; Meve & Albers, unpublished). A similar pattern is found in *Brachystelma* with averages of 0.78  $\mu\text{m}$  in *B. filifolia* and 1.48  $\mu\text{m}$  in *B. burchellii* (Meve & Liede, 2001a). Chromosomes in most species and genera of the Ceropegieae, however, have an average length of around 1  $\mu\text{m}$  (Fig. 1). Noteworthy outliers at the lower end are the genera *Duvaliandra* and *Leptadenia*. In the monotypic stapeliad genus *Duvaliandra* conspicuously small chromosomes (0.68  $\mu\text{m}$ ) were found. In *Leptadenia* (two species investigated, cf. Appendix 1), the average length is 0.72  $\mu\text{m}$  (Meve & Albers, unpublished). Relatively large chromosome sizes are found in species expressing evolutionarily basic morphological characters (*Caralluma edulis*, *C. sinaica* [1.40  $\mu\text{m}$ , Huesmann, 1993], *Ceropegia sankuruensis* [1.37  $\mu\text{m}$ ; Meve, unpublished]). The largest chromosomes of the whole tribe (1.72  $\mu\text{m}$  on the average) were observed in *Neoschumannia kamerunensis* (Meve, 1997b). This strong twiner is isolated from all other species of the tribe by its 3-seriate corona. Meve (1995b) considered *Neoschumannia* to be primitive in the Ceropegieae based on morphological characters. With-



in the Ceropegieae, genera with a twining, non-succulent habit, such as *Heterostemma*, *Leptadenia*, or *Orthanthera*, form a heterogeneous assemblage around the stapeliads and their relatives such as *Brachystelma* and *Ceropegia*. In contrast to *Ceropegia* and the stapeliads, chromosomes in *Heterostemma*, *Leptadenia*, and *Orthanthera* are on average ca. 0.25  $\mu\text{m}$  smaller.

The smallest chromosomes, however, are found in the Asclepiadeae (Fig. 1), in particular the subtribes Asclepiadinae, Astephaninae, Metastelminae, and Oxypetalinae (ranging from 0.7 to 1.15  $\mu\text{m}$  on the average). Usually, their chromosomes are less than 1  $\mu\text{m}$  long. Only in one subtribe of the Asclepiadeae, the Gonolobinae, are chromosomes on the average larger than 1.05  $\mu\text{m}$ .

Comparing average chromosome lengths in the three subfamilies as well as those for the tribes of the Asclepiadoideae, a general tendency of size reduction can be seen (Figs. 1, 2). Stepwise, starting with the presumably most primitive subfamily Periplocoideae to the higher evolved Asclepiadoideae, and within the latter subfamily starting with the most primitive Fockeeae to the most advanced Asclepiadeae, a decrease in chromosome size has taken place (Fig. 1). Chromosome size evolution recurs in a similar pattern within lower units such as subtribes or groups of related genera as such as the stapeliads.

## 2C DNA VALUES

The relative 2C DNA values for over 30 taxa of *Caralluma*, *Ceropegia*, *Duvalia*, *Orbea*, *Stapelianthus*, and *Tridentea* have been cytophotometrically determined in our lab and compared to the average karyotype lengths (cf. Huesmann, 1993). All our studies showed a good correlation between the two parameters of DNA content and chromosome size. For example, in the *Caralluma* complex we found for *C. umbellata* 0.82 pg/20.4  $\mu\text{m}$ , *C. diffusa* 1.18 pg/27.6  $\mu\text{m}$ , *C. europaea* 1.38 pg/33.7  $\mu\text{m}$ , *C. sarkariae* 1.43 pg/18.9  $\mu\text{m}$ , *C. turneri* 1.50 pg/24.3  $\mu\text{m}$ , and for *C. edulis* 1.83 pg/27.8  $\mu\text{m}$  (Huesmann, 1993). The differences between some of these values are considerable, supporting, for example, the separation of *Caralluma* s.l. into a handful of smaller genera as will be proposed by Meve and Liede (unpublished) based on DNA sequence data. Determinations of 4C DNA values, as investigated by Pattnaik et al. (1997) for six stapeliad species, were not studied by us. Whereas the karyotype lengths measured by these authors are in the range of our results, the DNA values estimated are by far higher

than ours. The reasons for these deviations are unclear.

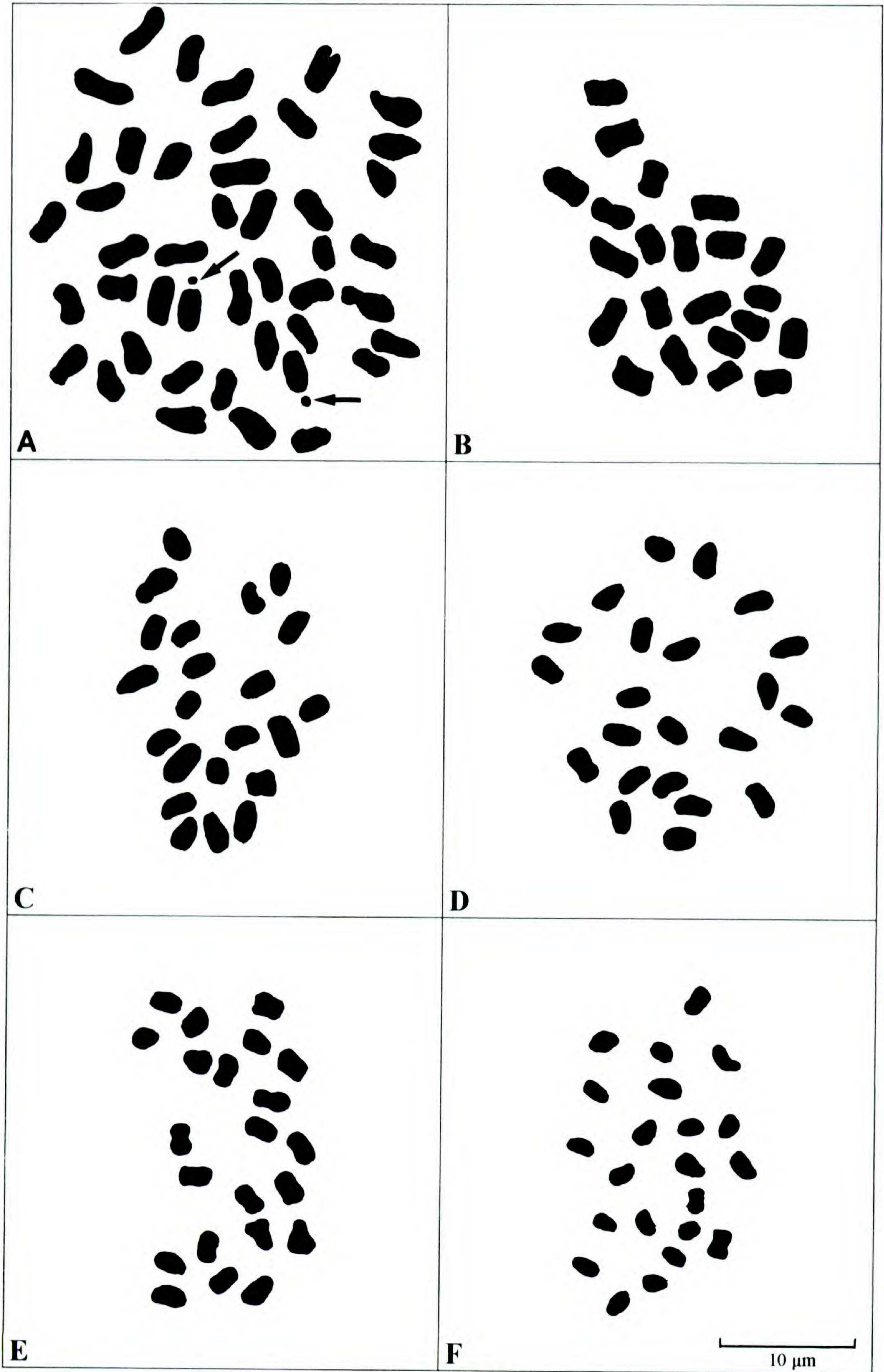
## GEOGRAPHICAL DISTRIBUTION OF DIFFERENT BASIC CHROMOSOME NUMBERS

We have contributed most to the karyological knowledge in African Asclepiadoideae since the emphasis of our ongoing study was on the Ceropegieae. In contrast, in other regions of the world there are still many gaps in the data. Despite this geographically biased data set of basic chromosome numbers, some summary can be made to show their diversity in the different regions of the world (Table 2).

The Asclepiadoideae are worldwide in distribution, whereas the primitive Periplocoideae and Secamonoideae are restricted to the Old World. Notably, all taxa investigated of the latter two subfamilies, and also the basal Fockeeae of the Asclepiadoideae, have  $x = 11$ , large chromosomes, and they all come from Africa (only one species from Arabia).

In Europe, Madagascar, and Australia only the basic number  $x = 11$  is known. In the best studied area, Africa, just a single genus, the southern African *Microlooma*, has the deviating basic chromosome number of  $x = 10$  (Albers et al., 1993). The African *Pentarrhinum insipidum* is variable in its basic chromosome number ( $x = 9, 11$ , and 12), although the  $2n = 18$  reported from Burundi (Renard et al., 1983) remains mysterious because otherwise only increased numbers have been found for this species. Additionally,  $x = 13$  has been counted once by Bramwell et al. (1972) for *Calotropis procera* from the Cape Verde Islands, whereas Borgen (1975) confirmed the counts of  $x = 11$  found also by other authors (e.g., Bhattacharya et al., 1971). We also counted  $x = 11$  for the same taxon and even from Cape Verde. In all cases where counts of  $2n = 24$  have been found, 2 B-chromosomes are most likely responsible, due to their inconsistency of occurrence; variation between  $2n = 22$  and  $2n = 24$  occurs among populations (*Pentarrhinum insipidum*) and also within populations (e.g., *Brachystelma mertonii*, Appendix 1) corroborating this concept (cf. Rees, 1974). One or two B-chromosomes have been found to occur commonly in *Hoya* (Nakamura, 1993). In Asia the percentage of species with deviating numbers ( $x = 12$  have been reported for, e.g., *Heterostemma tanjorensis* Wight & Arn. [Navaneetham, 1981] or *Tylophora asthmatica* Wight & Arn. [Sreedevi & Namboodiri, 1977]), is slightly higher than in the rest of the Old World, but strikingly different from the situation found in







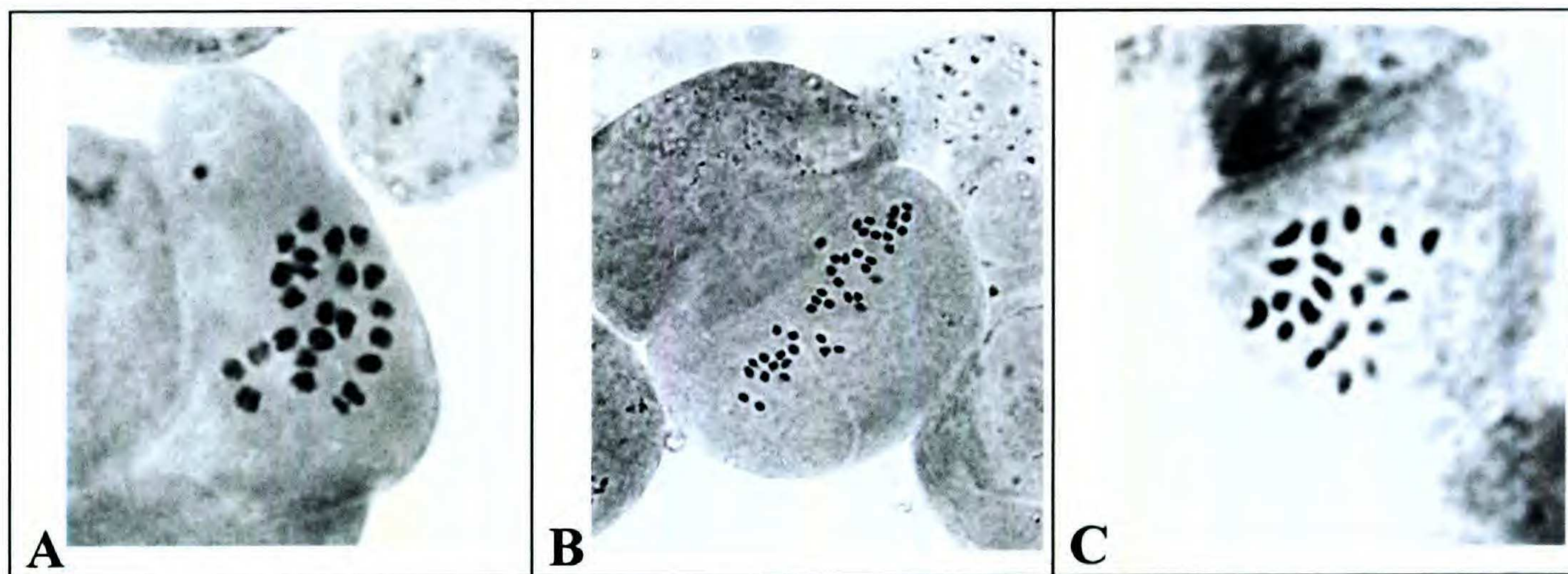


Figure 3. Mitotic metaphase chromosomes of Asclepiadoideae in the light microscope. —A. *Ceropogia cumingiana*,  $2n = 22$  (Liede 3250). —B. *Caralluma adscendens* var. *gracilis*,  $2n = 44$  (Sarkaria 32-90). —C. *Microloma incanum*,  $2n = 20$  (Albers & Meve 88). (A: ca. 1350 $\times$ ; B: ca. 500 $\times$ ; C: ca. 2400 $\times$ ; for vouchers see Appendix 1.)

the New World (Table 2). Here, one fifth of the species in North America (incl. Mexico) and more than one third in southern Central and South America have derived, predominantly decreased numbers (e.g., *Grisebachiella*, *Orthosia*, *Philibertia*; Appendix 1). It seems that chromosomal evolution with respect to the basic numbers has begun a new stage in the New World.

#### DISCUSSION

Different basic chromosome numbers often discriminate a taxon into separate taxonomical subunits such as families, tribes, or genera (various examples are given in Stace, 1989). Many studies have demonstrated the taxonomic value of basic chromosome numbers even at infrageneric level (e.g., *Pelargonium*: Albers et al., 1992; *Moraea*: Goldblatt, 1971, 1986). As van der Laan and Arends (1985) indicated, the basic number  $x = 11$  is the most frequent number in Apocynaceae s. str. (Apocynoideae & Rauvolfoideae). Approximately 60% of the species they studied have this number, but 40% deviate (van der Laan & Arends, 1985). The numbers  $x = 10, 9, 8, 7$ , and 6 have evolved by descending aneuploidy, whereas  $x = 12$  is an increasing number (van der Laan & Arends, 1985). One fifth of all studied species contain the deviating number  $x = 9$ . This high proportion might be

inflated by the relatively high number of karyologically studied species in the genera *Pachypodium* and *Strophanthus*. At present karyological information is only available for 241 species (14%) of Apocynaceae s. str. from 73 genera (40%) (van der Laan & Arends, 1985; Albers, unpublished data). Although this rate seems rather poor, it represents quite a typical situation for a family with predominantly woody species (e.g., Ehrendorfer, 1982).

The only basic chromosome number in the Periplocoideae and Secamonoideae is  $x = 11$ , which is also by far the most common situation in the Asclepiadoideae. Comparing these basic chromosome numbers with those of the Apocynaceae s. str. there is one striking difference: deviating basic chromosome numbers occur much less frequently in Asclepiadoideae with only about 4% compared with 40% in the other two subfamilies Apocynoideae and Rauvolfoideae.

The relatively frequent occurrence of different basic numbers in various tribes and subtribes of both Apocynoideae and Rauvolfoideae points to parallel genome evolution (van der Laan & Arends, 1985). The main developments have taken place repeatedly but independently.

In Apocynaceae s. str. polyploidy is only known to occur in nine genera (van der Laan & Arends, 1985). In total, 13% of the Apocynaceae s. str. are

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Figure 2. Squash preparations of mitotic metaphase plates (camera lucida drawings). —A. Periplocoideae: *Raphionacme hirsuta* ( $2n = 44$ , two satellites marked by arrows, Venter 9110). —B. Secamonoideae: *Secamone punctulata* ( $2n = 22$ , Hemp s.n.). —C. Asclepiadoideae, Fockeeae: *Cibirhiza dhofarensis* ( $2n = 22$ , Butler s.n.). —D. Asclepiadoideae, Marsdenieae: *Telosma accedens* ( $2n = 22$ , Schneidt 96-45). —E. Asclepiadoideae, Ceropegieae: *Angolluma denboefii* ( $2n = 22$ , Masinde 889). —F. Asclepiadoideae, Asclepiadinae: *Sarcostemma viminale* subsp. *odontolepis* ( $2n = 22$ , Meve & Liede 3354). (Bar = 10  $\mu$ m; for vouchers see Appendix 1.)



Table 2. Geographical distribution of basic chromosome numbers in Periplocoideae, Secamonoideae, and Asclepiadoideae (Apocynaceae).

Region	No. of taxa <sup>1</sup>	Basic chromosome numbers of karyologically known taxa in percentages					
		x = 9	x = 10	x = 11	x = 12	x = 13	x = 14
Old World							
Africa & Arabia	496	0.2	0.8	98.6	0.2	0.2	—
Europe	9	—	—	100	—	—	—
Asia	83	—	—	95.2	4.8	—	—
Australia	9	—	—	100	—	—	—
Madagascar	63	—	—	100	—	—	—
New World							
North America incl. Mexico	37	—	18.9	81.1	—	—	—
S Central & South America	30	10	23.3	63.4	—	—	3.3

<sup>1</sup> Each taxon is scored in every region of its occurrence.

polyploids, which is comparatively little (cf. Morton, 1966). All basic chromosome numbers are involved in different polyploid series. The highest number ever counted are the ca. 180 chromosomes of *Alyxia* (van der Laan & Arends, 1985). The situation in Asclepiadoideae is very similar, but the degree of polyploids is even lower, with only around 6%. Only in the Ceropegieae, which are dominated by the stem-succulent stapeliads, does polyploidy increase to about 10%, supporting the old hypothesis of the better ability of polyploids at colonizing new areas and being more hardy in less favorable habitats (e.g., Stebbins, 1985). However, compared to the 27.9% polyploid taxa in Cactaceae (Pinkava et al., 1985), it cannot be argued that polyploidy really played an important role in stapeliad evolutionary history. This might be true only on a more regional scale. The stapeliads had their evolutionary center in northeastern Africa (Meve, 1997a), but they formed a secondary center in southern Africa, where the majority of stapeliad polyploids are distributed (Albers, 1983; Albers & Meve, 1991, unpublished data). Here, rapid speciation took place accompanied not by derivation of chromosome number but instead by an increase in polyploidization events. This means that speciation here has taken place only at the level of chromosome and not of the karyotype (genome evolution). In contrast, the Apocynaceae s. str. have been more successful with derived numbers (karyotype evolution).

Tetraploidy is by far the most frequent polyploid condition in both Apocynaceae s. str. and Asclepiadoideae. In general, the tetraploid condition is considered to be the most successful in higher plants (DeWet, 1980). Even Cactaceae do not depart from this, since infraspecific polyploidy, main-

ly based on autopolyploidy, is rare in the entire family (cf. Pinkava et al., 1985).

Van der Laan and Arends (1985) observed that most chromosomes of Apocynaceae s. str. (Apocynoideae and Rauvolfioideae) species fall in the range of 1 to 2  $\mu\text{m}$  in length. Considerably longer chromosomes are found only in the tribes Alstonieae and Plumerieae (*Vallesia* and *Allamanda*, up to 3  $\mu\text{m}$  long) and Tabernaemontaneae (*Tabernaemontana* and *Voacanga*, up to 3.5  $\mu\text{m}$  long) of the Rauvolfioideae (data extracted from van der Laan & Arends, 1985; tribal disposition sensu Endress & Bruyns, 2000), and could indicate a similar trend in Asclepiadoideae, with larger chromosomes being predominantly confined to basal taxonomic units. On the average, however, there is no noticeable difference in chromosome length between the two subfamilies of Apocynaceae s. str. In both, average chromosome length is around 1.5  $\mu\text{m}$ . The chromosomes of the generally woody Apocynaceae s. str. can be considered as small and are in the same range as those of the Periplocoideae, Secamonoideae, and some tribes of the Asclepiadoideae. Pattnaik et al. (1997), Raynaud (1991), and Nakamura (1991) published measurements of similar sizes for some stapeliads. However, the analysis of Pattnaik et al. (1997: Table 1, p. 89) revealed larger rather than smaller chromosomes in tetraploids as compared with diploids. For example, Pattnaik gave the karyotype length for *Orbea paradoxa* as 61.54  $\mu\text{m}$ , whereas we measured 42.91  $\mu\text{m}$  (Albers & Meve, unpublished). This surprising difference, which is even higher when comparing tetraploids with diploids of *Orbea variegata*, remains unexplained.

Comparing chromosome size in the Periplocoideae, Secamonoideae, and Asclepiadoideae, on av-



erage the size of the karyotype diminishes stepwise starting with rather large chromosomes in the basal Periplocoideae and ending with the smallest karyotype length in the presumedly most advanced tribe of the Asclepidoideae, the Asclepiadeae. In the asclepiads reduction of the genome size ( $x = 10$ ,  $x = 9$ ) is restricted to the tribe Asclepiadeae, which is also the only group characterized by having pendent pollinia. All other taxa (Secamonoideae, Fockeeae, Marsdenieae, and Ceropegieae) have the conserved  $x = 11$ , and are characterized by having erect pollinia. The erect position of pollinia has been shown to represent the primitive state in Asclepiadoideae by Kunze's (1993) careful morphological analysis. Within the tribe Asclepiadeae, subtribe Gonolobinae can be regarded as the karyologically most primitive, since its chromosomes are on the average slightly more than 1  $\mu\text{m}$  long—the largest in Asclepiadeae, and approaching the length of those in the Ceropegieae. Gonolobinae also do not have numbers deviating from  $x = 11$ . This is an interesting result for the systematics of the subfamily Asclepiadoideae, since erect as well as more or less pendent, but mostly horizontally arranged pollinia have been reported for the Gonolobinae (cf. Kunze, 1995). Thus, both pollinarium morphology as well as karyological data provide evidence for a basal position of the Gonolobinae within the Asclepiadeae, and the results of the large cp DNA study by Potgieter and Albert (2001 this volume) do not refute this. Because they are restricted to the most advanced groups of the Asclepiadoideae, the subtribes Astephaninae, Metastelminae, and Oxypetalinae of Asclepiadeae, we regard reductions in the basic chromosome number as a relatively recent step in genome evolution within Asclepiadeae, which has taken place in parallel in the Old World (Astephaninae) and the New World (Metastelminae and Oxypetalinae).

Variation in the karyotype length is not restricted to the tribal level; it is also widespread at the generic level. In large genera, e.g., *Ceropegia* and *Brachystelma*, karyotype lengths can vary considerably from species to species, without compromising the generic affiliation of species with deviating chromosome size, such as *Brachystelma* (*Macropetalum*) *burchellii* (cf. Meve & Liede, 2001a). In small genera or groups of species considerable differences in chromosome size between the species might, however, question congeneric treatments. For example, the inclusion of *Larryleachia* (1.40  $\mu\text{m}$ /chromosome length on average) in *Lavrania* (0.91  $\mu\text{m}$ ), as proposed by Bruyns (1999), is rejected by Meve and Liede (2001b). And in *Caralluma* s.l. karyotype length analysis will support new

taxonomic solutions for this heterogeneous assemblage of species. In particular, *C. edulis* (ca. 1.5  $\mu\text{m}$ ) and *C. sinaica* (ca. 1.3  $\mu\text{m}$ , Albers & Meve, unpublished data), which came out as a separate group in molecular studies (Meve & Liede, unpublished data), are additionally characterized by their large chromosomes. As to the direction in chromosome size evolution (from large to small) in the Asclepiadoideae as postulated above, the results we have for *Neoschumannia* support our ideas. *Neoschumannia*, which has the largest chromosomes in subfamily Asclepiadoideae (1.72  $\mu\text{m}$  in *N. kamerunensis*) but a complex corona that is 3-seriate, has been regarded as a primitive member of the Ceropegieae (Meve, 1995b, 1997b).

In Marsdenieae we again have support for the hypothesis that basal taxa tend to have large chromosomes, since Omlor (1998) regarded the genera *Marsdenia* and *Telosma* (those with large chromosomes) as basal in the tribe. In contrast, the highly diverse and specialized Asian/Australian genus *Hoya*, where many of the up to 300 species (Forster et al., 1998) show derived features as such as herbaceous epiphytic growth, succulent leaves, clear latex, and a germination crest along the inner edge of the pollinium, possesses rather small chromosomes (0.91  $\mu\text{m}$  on average for the genus, Fig. 1; for sizes of *Hoya* chromosomes see also Nakamura, 1992, 1993).

Considering the distribution patterns of basic chromosome numbers and of the different karyotype sizes in Asclepiadoideae, our data suggest Africa as the common area where (karyotype) evolution began. This conclusion coincides with that of van der Laan and Arends (1985) for Apocynoideae and Rauvolfioideae, where most of the genera with derived basic chromosome numbers occur outside the African continent (cf. *Catharanthus* and *Apocynum* ( $x = 8$ ) in Madagascar, the Middle East, and North America; *Plumeria* and *Allamanda* ( $x = 9$ ) in the Americas; *Odontadenia* and *Beaumontia* ( $x = 12$ ) in America and Asia). Of the ca. 40 genera of Apocynaceae s. str. occurring in Africa, 35 have been karyologically investigated. Of these, only 3 are not characterized by  $x = 11$ , again supporting the idea of an African origin of the Apocynaceae s.l.

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Appendix 1. New chromosome numbers in Periplocoideae, Secamonoideae, and Asclepiadoideae (Apocynaceae). The table is differentiated in the two categories: (1) New and first chromosome counts for taxon (unmarked); and (2) New counts confirming previous chromosome numbers (marked by #); additionally, taxa marked by an asterisk (\*) served as vouchers for chromosome size analysis, but their chromosome numbers were published previously.

Taxon	2n	Locality	Voucher
<b>PERIPLOCOIDEAE</b>			
<b>Camptocarpus Decne.</b>			
<i>C. crassifolius</i> Decne.	22	MADAGASCAR: s. loc.	Petignat s.n. [ULM]
<b>Cryptolepis R. Br.</b>			
<i>C. decidua</i> (Planch. ex Hook. f. & Benth.) N. E. Br.	22	NAMIBIA: Warmbad	Verhoeven 203
<i>C. oblongifolia</i> (Meisn.) Schltr.	22	R.S.A.: Eastern Cape Prov., Vredefort	du Preez s.n.
<i>C. sanguinolenta</i> (Lindl.) Schltr.	22	NIGERIA: s. loc.	ex hort. BG MSUN [MSUN]
<b>Cryptostegia R. Br.</b>			
<i>C. madagascariensis</i> Bojer ex Decne.	22	s. loc.	ex hort. MSUN
<b>Ectadium E. Mey.</b>			
<i>E. virgatum</i> E. Mey. var. <i>virgatum</i>	22	NAMIBIA: 16 km O Lüderitz	Albers 2413 [MSUN]
<b>Mondia Skeels</b>			
<i>M. whitei</i> (Hook. f.) Skeels	22	TANZANIA: S slope Mt. Kilimanjaro, Msaranga Valley	Liede & Meve 3351 [UBT]
<b>Periploca L.</b>			
<i>P. aphylla</i> Decne.	22	ISRAEL: Daragoth (Dead Sea Area), near road to Ma'aleh	Avishai s.n.
<i>P. viscidiformis</i> K. Schum.	44	YEMEN: Jabal Haraz, ca. 25 km S Manákhah	Mangelsdorff Y15 [in hort UBT]
<b>Petopentia Bullock</b>			
<i>P. natalensis</i> (Schltr.) Bullock	22	ex hort. Kiel	ex hort. Kiel
<b>Raphionacme Harv.</b>			
<i>R. brownii</i> Scott-Elliott	22	IVORY COAST (STATE): Korbogo, Granitinselberg (IB2)	Porembski & Biedinger 1488 [MSUN]
<i>R. flanaganii</i> Schltr.	22	R.S.A.: Kwazulu-Natal, Pietermaritzburg, S Ashburn Stn.	Albers & Balkwill in K 1577 [MSUN]
<i>R. globosa</i> K. Schum.	22	TANZANIA: Ruvuma Prov.	Specks 286 [MSUN]
<i>R. hirsuta</i> (E. Mey.) R. A. Dyer	44	R.S.A.: Northern Prov., Sterkfontein caves	Venter 9110
<i>R. lanceolata</i> Schinz	22	IVORY COAST (STATE): s. loc.	Porembski 271 [MSUN]
<i>R. madiensis</i> S. Moore	22	TANZANIA: Ruvuma Prov., Namchwea Hill	E. & M. Specks 494 [MSUN]
<i>R. palustris</i> Venter & R. L. Verh.	44	R.S.A.: s. loc.	Stork 24 ex hort MSUN
<i>R. splendens</i> Schltr.	22	TANZANIA: s. loc.	Specks 692 [MSUN]
<b>Schlechterella K. Schum.</b>			
<i>S. abyssinica</i> (Chiov.) Venter & R. L. Verh.	22	KENYA: Forole	Newton 4555 [EA]



Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<b>Stomatostemma N. E. Br.</b>			
<i>S. monteiroae</i> N. E. Br.	22	s. loc.	s.n. sub IPPS 1427 [MSUN]
<b>Tacazea Decne.</b>			
<i>T. apiculata</i> Oliv.	22	R.S.A.: Northern Prov.	Venter 9188 [K]
<b>SECAMONOIDEAE</b>			
<b>Secamone R. Br.</b>			
<i>S. alpinii</i> Schult.	22	R.S.A.: Western Cape Prov., Leipoldt's Grave	Liede 2548
<i>S. filiformis</i> (L. f.) J. H. Ross	22	R.S.A.: Northern Prov., Venda	Liede 632 [K, MSUN]
<i>S. parviflora</i> (Oliv.) Bullock	22	KENYA: Kwale, Shimoni	Liede & Newton 3196 [E, MSUN, ULM]
<i>S. parviflora</i> (Oliv.) Bullock	44	KENYA: Kilifi, GEDE National Monument	Liede & Newton 3198
<i>S. punctulata</i> Decne.	22	TANZANIA: Moshi, Lake Chala	A. & C. Hemp s.n. [UBT]
<b>ASCLEPIADOIDEAE</b>			
<b>Tribe: FOCKEEAE</b>			
<b>Cibirhiza Bruyns</b>			
* <i>C. albersiana</i> Kunze, Meve & Liede	22	TANZANIA: Dodoma Prov., 5 km S Mpwapwa	Specks 248
<i>C. dhofarensis</i> Bruyns	22	OMAN: Dhofar, 25 km W Salalah	Butler s.n. [UBT]
<b>Fockea Endl.</b>			
<i>F. angustifolia</i> K. Schum.	22	ZIMBABWE: Hwange, Deka Matetsi	Albers & Meve 524
<i>F. capensis</i> Endl.	22	R.S.A.: Western Cape Prov., s. loc.	ex hort, Kiel [MSUN]
<i>F. edulis</i> (Thumb.) K. Schum.	22	R.S.A.: s. loc.	s. coll. [MSUN]
<i>F. sinuata</i> (E. Mey.) E. A. Bruce	22	R.S.A.: Eastern Cape Prov., Willowmore	Bruyns 5075
<b>Tribe: MARSDENIEAE</b>			
<b>Cionura Griseb.</b>			
<i>C. erecta</i> (L.) Griseb.	22	TURKEY: Side, Manaugat	Heyne 120 [UBT]
<b>Dischidia R. Br.</b>			
<i>D. bengalensis</i> Colebr.	22	s. loc.	Cumming s.n. [MSUN]
<i>D. hirsuta</i> L.	22	PHILIPPINES: Quezon Natl. Park	S. Schneidt s.n. [ULM]
<i>D. (Dischidiopsis) luzonica</i> Schltr.	22	PHILIPPINES: Mt. Makiling	Liede 3262
<i>D. nummularia</i> Blume	22	PHILIPPINES: Quezon Natl. Park, from Pagbilao to Atimonan	Schneidt & Liede 96-18 [MSUN]



## Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<b>Dregea E. Mey.</b>			
<i>D. rubicunda</i> K. Schum.	22	KENYA: GEDE National Monument, Kilifi	Liede & Newton 3199 [ULM]
<i>D. schimperii</i> (Decne.) Bullock	22	ZIMBABWE: Thomson Junction between Victoria Falls and Hwange	Albers, Liede & Meve 520
<b>Gymnema R. Br.</b>			
# <i>G. sylvestre</i> R. Br.	22	CAMEROON: 20 km E Mokolo	Meve 919 [B, UBT]
<b>Hoya R. Br.</b>			
<i>H. australis</i> R. Br. ex Traill	22	s. loc.	van Donkelaar s.n. [in hort UBT]
<i>H. camphorifolia</i> Warburg	22	PHILIPPINES: Quezon, Quezon National Park	Schneidt 96-20 [UBT]
<i>H. heuschkeliana</i> Kloppenburg	22	PHILIPPINES: Luzon, Lake Bulusan	Schneidt 96-96 [UBT, ULM]
# <i>H. longifolia</i> Wall.	22	ex hort. BG Münster	Helmcker s.n. [in hort MSUN]
<i>H. meliflua</i> Merr.	22	PHILIPPINES: Luzon, Mt. Makiling	Liede 3274 [MSUN, ULM]
<b>Marsdenia R. Br.</b>			
<i>M. linearis</i> Decne.	22	CUBA: s. loc.	s. coll.
<i>M. megalantha</i> Goyder & Morillo	22	BRAZIL: Bahia, Mun, Iramaia, 42 km W Martacas towards Iramaia	Taylor et al. 1557 [K. MO, MSUN]
<i>M. rostrata</i> R. Br.	22	AUSTRALIA: NSW, 2 km S Kioloa	Meve & Hellbrügge 791 [MSUN]
<b>Telosma Coville</b>			
<i>T. cordata</i> Merr.	22	PHILIPPINES: Luzon, Alaminos, Hundred Islands Natl. Park	Schneidt & Liede 96-105 [AUH]
<i>T. accedens</i> Blume	22	PHILIPPINES: Laguna Prov. Mt Makiling	Schneidt 96-45 [UBT]
<b>Tribe: CEROPEGIEAE</b>			
<b>Angolluma Munster</b>			
<b>(= <i>Pachycymbium</i> Leach p.p., = <i>Stultitia</i> Phillips)</b>			
# <i>A. abayensis</i> (M. G. Gilbert) Plowes cf.	22	ETHIOPIA: Lake Abaye	Frank 64 [MSUN]
<i>A. commutata</i> (A. Berger) Plowes	22	SAUDI ARABIA: s. loc.	Collenette 8255
# <i>A. decaisneana</i> (Lem.) L. E. Newton	22	ALGERIA: Tassile (Sahara)	Plowes 3971
<i>A. denboefii</i> (Lavranos) Plowes	22	TANZANIA: Himo	Masinde 889 [UBT]
<i>A. eremastrum</i> Schwartz	22	YEMEN: 20 km E Al Dann	Mangelsdorff Y25 [ULM]
<i>A. hesperidum</i> (Maire) Plowes	22	MOROCCO: 36 km from Taquist, 1 km above Torres-de-Alcalá	i'Hart 67-106B [MSUN]
<i>A. laikipiensis</i> (M. G. Gilbert) Plowes	22	KENYA: 43 km NE Rumuruti	Newton 4221 [MSUN]



Appendix I. Continued.

Taxon	2n	Locality	Voucher
# <i>A. laticorona</i> (M. G. Gilbert) Plowes	22	ETHIOPIA: 2 km S Modjo, SHEWA	Gilbert s.n. sub <i>Plowes</i> 7695 [MSUN]
# <i>A. lugardii</i> (N. E. Br.) Plowes	22	R.S.A.: Northern Cape Prov., 20 km N Bladgrond	Meve & Liede 613 [MSUN]
<i>A. sacculata</i> (N. E. Br.) Plowes	22	SAUDI ARABIA: s. loc.	s. coll., s.n.
# <i>A. schweinfurthii</i> (Berger) Plowes	22	TANZANIA: s. loc.	Specks 805
<i>A. semitubiflora</i> L. E. Newton	22	TANZANIA: Kisite Crater	Newton 3419 [K, EA, MSUN]
# <i>A. subterranea</i> (E. A. Bruce & P. R. O. Bally) Plowes	22	KENYA: Mt. Maktau	Meve et al. 946 [MSUN]
# <i>A. tubiformis</i> (E. A. Bruce & P. R. O. Bally) Plowes	22	KENYA: 5 km N Longobito	Meve, Newton & Goyder 958
<i>A. vibratilis</i> (E. A. Bruce & P. R. O. Bally) M. G. Gilbert	44	KENYA: 36 km N Horr	Cumming 1443 [MSUN]
# <i>A. wissmannii</i> (O. Schwartz) Plowes	22	OMAN: Sarfait road, 4 km E of turn to Rakhyut	Jonkers 66 [MSUN]
<b><i>Brachystelma</i> Sims</b>			
<i>B. barberae</i> Harvey ex Hook. f.	22	ZIMBABWE: W Bulawayo	Albers 2570 [MSUN]
* <i>B. bracteolatum</i> Meve	22	NIGERIA: Jos Plateau	Specks 549 [K, MSUN]
<i>B. buchananii</i> N. E. Br.	22	TANZANIA: Ruvuma	Specks 378 [MSUN]
<i>B. burchellii</i> (Decne.) Peckover	22	R.S.A.: Free State, Bloemfontein	sub <i>Specks</i> 3156 [MSUN, UBT]
<i>B. christiana</i> Peckover	22	R.S.A.: KwaZulu-Natal	sub <i>Specks</i> 2531 [MSUN]
<i>B. decipiens</i> N. E. Br.	22	R.S.A.: Eastern Cape, Transkei	sub <i>Specks</i> 2390 [MSUN]
<i>B. filifolium</i> Schltr.	22	s. loc.	ex hort. [MSUN]
# <i>B. gracile</i> E. A. Bruce	22	ZIMBABWE: Bulawayo, Hyde Park	Albers 2558
<i>B. kituloensis</i> Goyder	22	TANZANIA: Makinda, Livingstone Mts.	Specks 599 [MSUN]
<i>B. lancasteri</i> C. Boele	22	ZIMBABWE: Bulawayo outskirts	Albers 2573 [MSUN]
<i>B. lineare</i> A. Rich.	22	ETHIOPIA: 27 km SW Bah Dar	Specks 432 [MSUN]
<i>B. macropetalum</i> N. E. Br.	22	R.S.A.: s. loc.	sub <i>Specks</i> 2986 [MSUN]
<i>B. megasepalum</i> Peckover	22	TANZANIA: Ruvuma Prov., Kitobaloma	Specks 748 [MSUN]
<i>B. meyerianum</i> Schltr.	22	R.S.A.: Eastern Cape Prov., Transkei	sub <i>Specks</i> 2987 [MSUN]
# <i>B. mortonii</i> C. C. Walker	22	IVORY COAST (STATE): Comoé-Nationalpark, 6.5 km N Lola Plain	Porembski sub <i>MS</i> 651 [K, MSUN]
<i>B. nanum</i> N. E. Br.	22	R.S.A.: Mpumalanga	Peckover sub <i>Specks</i> 2988 [MSUN]
<i>B. remotum</i> R. A. Dyer	22	R.S.A.: Kwazulu-Natal, 45 km SE Wakkerstroom	Craib s.n.
<i>B. richardsii</i> Peckover	22	TANZANIA: Ruvuma Prov., Mhukuru	Specks 762 [MSUN]
<i>B. rubellum</i> (E. Mey.) Peckover	22	R.S.A. Kwazulu-Natal, Thornville, Tala Hill	Cumming 3565
<i>B. simplex</i> Schltr.	22	IVORY COAST (STATE): Comoé-Nationalpark, 6.5 km N Lola Plain	Porembski 8648 [MSUN]



Taxon	2n	Locality	Voucher
<b><i>Caralluma R. Br. s.l.</i></b>			
# <i>C. acutangula</i> (Decne.) N. E. Br.	22	KENYA: Archer's Post	Meve 964
# <i>C. adenensis</i> (Deflers) A. Berger	22	OMAN: Wadi Afal	Jonkers 85 [MSUN]
# <i>C. adscendens</i> (Roxb.) R. Br.	22	INDIA: Bangalore, Tahlly	Bruyns 5937
# <i>C. adscendens</i> var. <i>attenuata</i> Wight	22	INDIA: 72 km of Tirumyam direction of Madurai	Sarkaria J18-90 [MSUN]
# <i>C. adscendens</i> var. <i>fimbriata</i> (Wall.) Gravely & Mayur.	22	INDIA: Pasarny Ghat Distr., Wai-Mahableshwar Rd., 3-4 km beyond Wai	Sarkaria 166-77
<i>C. adscendens</i> var. <i>geniculata</i> Gravely & Mayur.	22	INDIA: Marathumalai Hill near Nagercoil	Sarkaria J30-90 [MSUN]
<i>C. adscendens</i> var. <i>gracilis</i> Gravely & Mayur.	22	INDIA: 9 km beyond Tirumykm, near Malai Kuddi Patti	Sarkaria 62-78
<i>C. adscendens</i> var. <i>gracilis</i> Gravely & Mayur	22/44	INDIA: Yercaud Hill	Sarkaria J 32-90 [MSUN]
<i>C. arabica</i> N. E. Br.	22	OMAN: Ra's al-Hamra	Jonkers 16 [ON]
# <i>C. arachnoidea</i> (P. R. O. Bally) M. G. Gilbert var. <i>arachnoidea</i>	22	KENYA: between Kabernat and Kapengunia	Hartmann & Newton 28406 [MSUN]
<i>C. baradii</i> Lavranos	22	SOMALIA: 34 km W Hobio	Lavranos et al. 23338 [UPS]
<i>C. bhupinderana</i> Sarkaria	22	INDIA: Palamkottai-Tuticorn Rd., base of Vallandu Hill	Sarkaria 28-90 [MSUN]
* <i>C. burchardii</i> N. E. Br. subsp. <i>burchardii</i>	130-132	SPAIN: Canary Islands, Fuerteventura, Betancuria, Bco. de Ajuy	Wiemers s.n. [MSUN]
* <i>C. burchardii</i> subsp. <i>maura</i> (Maire) Meve & F. Albers	66	MOROCCO: 28 km N Sidni Ifni	Jonkers 223
# <i>C. cicutricosa</i> (Deflers) N. E. Br.	22	YEMEN: Hammam Ali	Noltee 807 [MSUN]
# <i>C. crenulata</i> Wall.	22	INDIA: Bangalore-Kodai road, 2 km beyond Narsapur	Sarkaria 10-77 [MSUN]
# <i>C. dalzielii</i> N. E. Br.	22	CAMEROON: W Mindif, between Maroua and Mindif	Specks s.n.
# <i>C. dicapuae</i> Chiov. subsp. <i>dicapuae</i>	22	KENYA: Longobito	Meve 955
# <i>C. diffusa</i> (Wight) N. E. Br.	22	INDIA: Tamkur, near Sideshurai Ganga Temple Hill	Sarkaria 81-75
# <i>C. edithae</i> N. E. Br.	22	ETHIOPIA: S Dire Dawa	Frank 57 [MSUN]
# <i>C. edulis</i> (Edgew.) Benth. & Hook.	22	ex hort. Basel	s. coll. [MSUN]
<i>C. edwardsiae</i> (M. G. Gilbert) M. G. Gilbert	22	KENYA: near Turbi	Hartmann 21393 [MSUN]
# <i>C. europaea</i> (Guss.) N. E. Br. var. <i>europaea</i>	22	MOROCCO: 55 km from Nador on road to Guercif	i'Hart 67-33B [MSUN]
* <i>C. europaea</i> (Guss.) N. E. Br. var. <i>europaea</i>	22	SPAIN: Almeida, Capo de Gata	Albers 87-23-004-20 [MSUN]
# <i>C. europaea</i> var. <i>judaica</i> M. Zohary	22	ISRAEL: Har Hanegev (Jebel Hursha)	Chaouat s.n. [HUJ, MSUN]
<i>C. flava</i> N. E. Br.	22	OMAN: Dhofar, Jabal Qamar, on road to Sarfait	Jonkers 150 [MSUN]
# <i>C. foetida</i> E. A. Bruce	22	KENYA: NE Rumuruti, Kisima Ranch	Meve 950 [UBT]
<i>C. furta</i> P. R. O. Bally	22	DJIBOUTI: s. loc.	Butler D106 [MSUN]
<i>C. gracilipes</i> K. Schum.	22	TANZANIA: Pare	Specks 632 [MSUN]
# <i>C. indica</i> (Wight & Arn.) N. E. Br.	22	INDIA: 13 km beyond Tiruchirapalli in direction to Pudukkottai	Sarkaria J 11-90



Appendix I. Continued.

Taxon	2n	Locality	Voucher
# <i>C. joannis</i> Maire	66	MOROCCO: Aoulez, 35 km on the road Taliouine to Agadir	<i>de Wilde s.n.</i>
<i>C. lavrani</i> Rauh & Wertel	22	YEMEN: s. loc.	<i>Frank 119 [MSUN, UBT]</i>
<i>C. moniliformis</i> P. R. O. Bally	22	SOMALIA: 4.5 km N Galgallo	<i>Koenen &amp; Krapp 22678 [MSUN]</i>
# <i>C. munbyana</i> (Decne. ex Munby) N. E. Br.	22	SPAIN: Murcia	<i>Berthet s.n. [UBT]</i>
<i>C. pauciflora</i> (Wight) N. E. Br.	22	INDIA: Palamkottai	<i>Bruyns s.n.</i>
# <i>C. peckii</i> P. R. O. Bally	22	s. loc.	<i>Plowes 7948 [MSUN]</i>
<i>C. priogonium</i> K. Schum.	22	SOMALIA: 26 km N Mogadiscio, ca. 3 km NE Malad	<i>Koenen &amp; Krapp 49388 [MSUN]</i>
# <i>C. procumbens</i> Gravely & Mayur.	22	INDIA: Masuthuamalai Hill, South Travancore	<i>Sarkaria 108-77</i>
# <i>C. sarkariae</i> Lavranos & Frandsen	22	INDIA: 8 km W Madurai, Madurai-Usilampatti Road, base of Nagamalai hill	<i>Sarkaria 23-90</i>
* <i>C. sinaica</i> (Decne.) A. Berger	22	ISRAEL: Dead Sea, Dragot shore	<i>Bruyns 2484 [MSUN]</i>
<i>C. socotrana</i> (Balf. f.) N.E. Br.	22	SOMALIA: 3 km E Los Anod	<i>Lavranos s.n.</i>
# <i>C. speciosa</i> N. E. Br.	22	KENYA: Archer's Post	<i>Meve 965</i>
<i>C. staintonii</i> Hara	22	NEPAL: Jiamiri (Bheri River Valley)	<i>Bruyns 2515 [MSUN, K]</i>
# <i>C. stalagmifera</i> C. E. C. Fischer	22	INDIA: Tirumyam-Madurai, km 72.5	<i>Sarkaria J17A-90 [MSUN]</i>
# <i>C. subulata</i> (Forsk.) Decne.	44	YEMEN: 6 km N Bajil	<i>Barad 11705</i>
# <i>C. tuberculata</i> N. E. Br.	22	INDIA: 2 km NW Jammu (near Magkola-Kujagh)	<i>Sarkaria 43-75</i>
* <i>C. turneri</i> E. A. Bruce	22	KENYA: Lake Victoria	<i>Hartman &amp; Newton 28587 [MSUN]</i>
# <i>C. umbellata</i> Haw.	22	INDIA: Tiruchirapalli-Puddukotai road	<i>Sarkaria 55-77</i>
<b><i>Ceropegia</i> L.</b>			
<i>C. africana</i> R. Br. subsp. <i>africana</i>	22	R.S.A.: Kzwazulu-Natal Prov., Oribi-Gorge	<i>Balkwill K 1570</i>
<i>C. albisepta</i> Jum & H. Perrier	22	MADAGASCAR: betw. Antsirabe and Ambositra (W side of Col des Tapias)	<i>Lavranos et al. 29964 [MSUN]</i>
<i>C. arabica</i> H. Huber	22	YEMEN: Ussab al Ali	<i>Mangelsdorff Y26 [UBT]</i>
<i>C. aristolochioides</i> Decne. subsp.	22	KENYA: Rift Valley Province, Kajiado District, Alhi River	<i>Masinde 684 [MSUN]</i>
# <i>C. aristolochioides</i> Decne. subsp. <i>deftersiana</i> Bruyns	22	YEMEN: Wadi Rima, ca. 35 km W Madinat ash Shirq	<i>Mangelsdorff Y11 [MSUN]</i>
<i>C. bulbosa</i> Roxb. (" <i>C. vignalidiana</i> ")	22	ETHIOPIA: Harar, Mt. Achim	<i>Specks 429 [MSUN]</i>
<i>C. cimiciodora</i> Obermeyer	22	R.S.A.: s. loc.	<i>ex BG Bonn 2535 [MSUN]</i>
<i>C. crassifolia</i> var. <i>copleyae</i> (Bruce & Bally) H. Huber	22	KENYA: Nairobi, near Airport	<i>Masinde &amp; Meve M 874 [EA, MSUN]</i>
<i>C. cumingiana</i> Decne.	22	PHILIPPINES: Luzon, Mt. Makiling	<i>Liede 3250 [MSUN]</i>
* <i>C. dichotoma</i> Haw. subsp. <i>dichotoma</i>	22	SPAIN: Canary Islands, Tenerife, Punta de Teno	<i>Meve s.n. [MSUN]</i>



## Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<i>C. dimorpha</i> Humbert	22	MADAGASCAR: between Ihosy and Ranohira, 10.5 km to Ranohira	Liede 2638 [MSUN]
<i>C. distincta</i> N. E. Br. ("C. brevirostre")	22	TANZANIA: Amani	Liede & Meve 3379 [EA, UBT]
# <i>C. elegans</i> Wall.	22	INDIA: Konanad	Bruyns 5906 [MSUN]
<i>C. filiformis</i> (Burch.) Schltr.	22	R.S.A.: Northern Cape Prov., Loxton	Bruyns 6683
<i>C. gilgiana</i> Werderm.	22	TANZANIA: SW Itigi	M. & E. Specks 1 039 [MSUN, UBT]
<i>C. hermannii</i> Rauh & M. Teissier	22	MADAGASCAR: Tuléar, E de la Table	Petignat 455
<i>C. humbertii</i> H. Huber	22	MADAGASCAR: Montagne de Francais	Mangelsdorff M 22 [MSUN]
<i>C. intermedia</i> Wight	22	INDIA: Ebanad	Bruyns 5903
# <i>C. juncea</i> Roxb.	44	INDIA: Tasparc, Vizakapatnam	Bruyns s.n.
<i>C. lugardiae</i> N. E. Br.	22	NAMIBIA: Steinhausen, Farm Wunderland	Grabow s.n. sub As 103
<i>C. meleagris</i> H. Huber	22	INDIA: s. loc.	s.n. ex Shirley [MSUN]
<i>C. meyeri-johannis</i> Engl.	22	KENYA: Mt. Kasigau, SW side	Meve et al. 936 [K, MSUN]
<i>C. multiflora</i> Bak. subsp. <i>multiflora</i>	22	ZIMBABWE: Bulawayo, Hyde Park	Albers 2559
# <i>C. nilotica</i> Kotschy	22	MALAWI: Njakwa Gorge, S Rukuru River at road from E Kwendeni to Rumpi	Thiede 2151 [MSUN]
<i>C. occidentalis</i> R. A. Dyer	22	R.S.A.: Western Cape Prov., Strandfontein	v. Jaarsveld & Bruyns 2321 [MSUN]
<i>C. petignatii</i> Rauh	22	MADAGASCAR: 30 km N Tuléar, near Mora-Mora	ex Petignat 296 [MSUN]
<i>C. powysii</i> D. V. Field	22	KENYA: Mt. Maktau	Meve 941 [K, MSUN]
<i>C. racemosa</i> N. E. Br. subsp. <i>glabra</i> H. Huber	44	MADAGASCAR: Ankarana	Mangelsdorff M 27 [MSUN]
<i>C. racemosa</i> N. E. Br. subsp. <i>racemosa</i>	22	TANZANIA: Kilimanjaro, Lake Chala	Meve & Liede 3355 [EA, UBT]
# <i>C. rupicola</i> Deflers	22	YEMEN: Djebel Haraz	Mangelsdorff Y 13 [MSUN]
<i>C. sankuruensis</i> Schltr.	22	CAMEROON: Mt Cameroon, W Likombe	Meve 909 [K, MSUN]
<i>C. saxatilis</i> Jum. & H. Perrier	22	MADAGASCAR: Ankarana Mts., Montagne de Francais	Mangelsdorff s.n. [MSUN]
<i>C. simoneae</i> Rauh	22	MADAGASCAR: forest between Tishombé and Ihado	Rauh 73117 [HEID, MSUN]
<i>C. stapeliaeformis</i> Haw.	22	s. loc.	s.n. ex Palmengarten
<i>C. stentiae</i> E. A. Bruce	22	R.S.A.: North-West Prov., NW Potchefstroom	Albers et al. 3529 [MSUN]
* <i>C. striata</i> Meve & Masinde	22	MADAGASCAR: Antsirabe	Rauh 75007 [HEID, MSUN]
<i>C. subaphylla</i> K. Schum.	22	SAUDI ARABIA: Muhayl	Collenette 7307 [MSUN]
# <i>C. thwaitesii</i> Hook.	22	INDIA: Davikolam	Bruyns 5944
# <i>C. variegata</i> Decne.	22	KENYA: 3 km N Maralal	Masinde & Meve 871 [MSUN]
<b>Duvalia</b> Haw.			
* <i>D. angustiloba</i> N. E. Br.	22	R.S.A.: Western Cape Prov., 82 km E Beaufort West	Meve 319 [MSUN, NBG]
* <i>D. caespitosa</i> (Mass.) Haw. var. <i>caespitosa</i>	44	R.S.A.: Western Cape Prov., betw. Muiskraal and Barrydale, nr Kleindoornrivier	Albers & Meve 129 [MSUN]



Appendix I. Continued.

Taxon	2n	Locality	Voucher
* <i>D. caespitosa</i> (Mass.) Haw. var. <i>compacta</i> (Haw.) Meve	44	R.S.A.: Western Cape Prov., E VanRhyndorp	Meve 263 [MSUN]
* <i>D. elegans</i> (Mass.) Haw.	22	R.S.A.: Western Cape Prov., 7.5 km N McGregor	Meve 383 [MSUN]
* <i>D. immaculata</i> (Lückh.) Bayer ex L. C. Leach	66	R.S.A.: Western Cape Prov., Gouritzmond	Meve 401 [MSUN]
# <i>D. maculata</i> N. E. Br.	22	R.S.A.: Western Cape Prov., Sterkfontein	Bruyns 6289
# <i>D. sulcata</i> N. E. Br. subsp. <i>sulcata</i>	44	YEMEN: Lodar	Hanacek 286 [in hort. UBT]
<i>D. sulcata</i> N. E. Br. subsp. <i>somalensis</i> (Lavrano) Meve	22	DJIBOUTI: s. loc.	Butler D105
<b>Duvallandra M. G. Gilbert</b>			
# <i>D. dioscorides</i> (Lavrano) M. G. Gilbert	22	YEMEN: Socotra, Hadiboh	Orlando s.n. [UBT]
<b>Echidnopsis Hook. f.</b>			
<i>E. angustiloba</i> E. A. Bruce & P. R. O. Bally	22	KENYA: ca. 5 km N Longobito	Meve 959 [K, MSUN, UBT]
<i>E. archeri</i> P. R. O. Bally	22	KENYA: Nguruman Escarpment, Oloibitoto River near Hayton's Falls	Archer in Bally S325 [K, ZSS]
<i>E. ballyi</i> (M. Lapostolle) P. R. O. Bally	22	SOMALIA: s. loc.	Plowes 6609
<i>E. bihendulensis</i> P. R. O. Bally	22	SOMALIA: below the Sheik Pass at Bihendula	Reynolds 1956
<i>E. cereiformis</i> Hook. f.	22	SUDAN: Erkovit, Jebel Aulimi	Hartmann 21505 [MSUN]
# <i>E. dammaniana</i> Sprenger	22	KENYA: S Gatap	Hartmann & Newton 28557 [MSUN]
<i>E. globosa</i> Thulin & Hjertson	22	YEMEN: Hadramaut, 14 km from the turning to the Masila field	Thulin et al. 8248 [K, UPS]
# <i>E. leachii</i> Lavranos	22	TANZANIA: Dodoma	Specks 1264 [UBT]
# <i>E. malum</i> (Lavrano) Bruyns	22	SOMALIA: 40 km NE Mogadishu	Lavrano 23224A
# <i>E. mijerteina</i> Lavranos	22	SOMALIA: 2 km S Eil	Lavrano 8446
# <i>E. repens</i> R. A. Dyer & Verd.	22	KENYA: Mt. Maktaw	Meve 942
<i>E. scutellata</i> subsp. <i>australis</i> Bruyns	22	KENYA: Marsabit, N side of Gof Chjoba crater	Lavrano & Bleck 19527
<i>E. scutellata</i> subsp. <i>dhofarensis</i> Bruyns	22	OMAN: Dhofar Province, on road from Thamarit to Salalah, Agabat al Hatab	Miller 2811 [E]
# <i>E. scutellata</i> subsp. <i>planiflora</i> (P. R. O. Bally) Bruyns	22	ETHIOPIA: Jijiga, Marda Pass	Gilbert s.n. sub Plowes 4264
<i>E. scutellata</i> subsp. <i>planiflora</i> (P. R. O. Bally) Bruyns	44	SOMALIA: 4 km NW Erigavo	Lavrano 7325 [FT]
# <i>E. scutellata</i> (Deffers) A. Berger subsp. <i>scutellata</i>	22	YEMEN: road from Kuhlan to Hajjah	Miller & Long 3259 [E]
<i>E. sharpei</i> subsp. <i>ciliata</i> (P. R. O. Bally) Bruyns	22	SOMALIA: Sheik Pass	Bailes 134 [MSUN]
<i>E. sharpei</i> A. C. White & B. Sloane subsp. <i>sharpei</i>	22	KENYA: S Moyale	Hartmann & Newton 21381 [MSUN]



## Appendix 1. Continued.

Taxon	2n	Locality	Voucher
# <i>E. squamulata</i> (Decne.) P. R. O. Bally	44	YEMEN: Amiri Highlands, 6 km NE Dhala	Lavranos 1869 [K. PRE]
<i>E. urceolata</i> P. R. O. Bally	22	KENYA: s. loc.	Lavranos 12220
<i>E. urceolata</i> P. R. O. Bally	44	YEMEN: 15 km S Taizz (Aden road)	Lavranos & Newton 13101
<i>E. virchowii</i> K. Schum.	22	SOMALIA: s. loc.	Bailes sub Plowes 6610 [MSUN]
# <i>E. watsonii</i> P. R. O. Bally	44	SOMALIA: 8 km W Bawn	Lavranos 10421 [MSUN]
<i>E. yemenensis</i> Plowes	22	YEMEN: base of Menakha Pass near Suq al Khamis	Plowes & Barad 7764 [SRGH]
<b><i>Edithcolea</i> N. E. Br.</b>			
<i>E. grandis</i> N. E. Br.	22	KENYA: Ndi Area	Meve 932
<b><i>Heterostemma</i> Wight &amp; Arn.</b>			
<i>H. acuminatum</i> Decne.	22	AUSTRALIA: Port Curtis Distr., Olsens Caves	Forster 5090 [BRI, K. L. MEL, MO]
<i>H. herbertii</i> Elmer	22	PHILIPPINES: Luzon, Mt Makiling	Liede 3271b [UBT]
<b><i>Hoodia</i> Sweet ex Decne.</b>			
# <i>H. gordonii</i> (Masson) Sweet	22	NAMIBIA: ca. 30 km S Warmbad, Farm Eendoorn (Pretorius)	Meve & Struck 192 [MSUN]
<i>H. juttiae</i> Dinter	22	NAMIBIA: Vredenhof	Bruyns 3508 [MSUN]
<i>H. longispina</i> Plowes	22	NAMIBIA: Witpütz	Albers & Meve 85 [MSUN]
<i>H. officinalis</i> (N. E. Br.) Plowes subsp. <i>deletaiana</i> (Dinter) Bruyns	22	NAMIBIA: Klinghardt	Hammer 914
<i>H. pedicellata</i> (Schinz) Plowes	22	NAMIBIA: Rössingberge	Albers 2718 [MSUN]
<i>H. pillansii</i> N. E. Br.	22	R.S.A.: s. loc.	s. coll. sub Al 2510
<i>H. pilifera</i> (L. f.) Plowes subsp. <i>pilifera</i>	22	R.S.A.: Western Cape Prov., ca. 19 km SE Oudtshoorn	Meve 406 [MSUN]
# <i>H. ruschii</i> Dinter	22	NAMIBIA: Uri Hauchab	Jürgens 91245
<b><i>Huernia</i> R. Br.</b>			
<i>H. arabica</i> N. E. Br.	22	YEMEN: 3 km N Ar Rahida	Barad 11752 [MSUN]
<i>H. archeri</i> L. C. Leach	44	KENYA: 100 km W Malindi, Galana River, Lali Hill	Powys 804
# <i>H. aspera</i> N. E. Br.	44	KENYA: Mt Maktou	Meve 943b [MSUN]
<i>H. boleana</i> M. G. Gilbert	22	ETHIOPIA: N Addis Ababa, Bole Valley	Horwood 11072 [MSUN]
<i>H. brevirostris</i> N. E. Br. subsp. <i>brevirostris</i>	22	R.S.A.: Eastern Cape Prov., Steytlerville, Springbokvlakte	Lavranos & Pehlemann 19868
<i>H. erinacea</i> P. R. O. Bally	44	KENYA: between Moyale and Marsabit, Sololo hill	Cumming 1416
# <i>H. guttata</i> (Masson) Haw.	22	R.S.A.: Western Cape Prov., near Calitzdorp Dam	Leach & Rossouw 16147 [MSUN, NBG]
# <i>H. hallii</i> E. Lamb & B. M. Lamb	22	NAMIBIA: ca. 29 km E Aus, Farm Plateau	Meve & Struck 181 [MSUN]
# <i>H. humilis</i> (Masson) Haw.	22	R.S.A.: Eastern Cape Prov., Fraserburg, Tafelberg	LCL 17710
# <i>H. keniensis</i> R. E. Fries	44	KENYA: 30 km N Maralal	Meve 963 [MSUN]



Appendix I. Continued.

Taxon	2n	Locality	Voucher
# <i>H. keniensis</i> R. E. Fries var. <i>keniensis</i>	44	KENYA: Tugen Hills	Newton 4283
<i>H. keniensis</i> var. <i>nairobiensis</i> A. C. White & B. Sloane	22	KENYA: 4 km N Narock	Cumming 1032 [MSUN]
<i>H. lenewtonii</i> Plowes	22	KENYA: E Lake Turkana, Sul-Sul Mudde	Newton & Powys 3703 [EA, K]
# <i>H. nigeriana</i> Lavranos	22	NIGERIA: s. loc.	Plowes 7856 [MSUN]
<i>H. pendula</i> E. A. Bruce	22	R.S.A.: Eastern Cape Prov., Transkei, s. loc.	s. coll
# <i>H. penzigii</i> N. E. Br.	22	YEMEN: Taizz, 15 km NE Airport	Plowes 7803 [MSUN]
# <i>H. procumbens</i> (R. A. Dyer) L. C. Leach	44	R.S.A.: Mpumalanga, Masisi Village	Hardy 5404 [NMG]
# <i>H. reticulata</i> (Masson) Haw.	22	R.S.A.: Western Cape Prov., VanRhynsdorp, Giftberg	Lavranos 28207
<i>H. rosea</i> Newton & Lavranos	22	YEMEN: 5 km W Al Magrabah	Noltee 1528 [MSUN]
<i>H. rubra</i> Plowes	22	YEMEN: Ramadah	Noltee 2092 [MSUN]
# <i>H. saudi-arabica</i> D. V. Field	22	YEMEN: Taifa/Hadda	Lavranos & Collette 18467 [MSUN]
<i>H. thudichumii</i> L. C. Leach	22	R.S.A.: Eastern Cape Prov., s. loc.	Albers 2521 [MSUN]
# <i>H. verekeri</i> Stent var. <i>verekeri</i>	22	ZIMBABWE: NW Hwange, "Thomson Junction"	Albers, Liede & Meve 523 [MSUN]
# <i>H. volkartii</i> Peitsch, ex Werderm. & Peitsch. var. <i>volkartii</i>	44	ZIMBABWE: Buchwa, Old Iron Mine (Masvingo Distr.)	Erwee s.n. sub Albers 2574
<i>H. zebrina</i> N. E. Br. subsp. <i>magniflora</i> (Phillips) L. C. Leach	22	R.S.A.: Northern Prov., Zaaiplaats bei Potgietersrust, Tin-Mine	Balkwill K 1567
# <i>H. zebrina</i> n. E. Br. subsp. <i>zebrina</i>	22	R.S.A.: 23°23'S, 29°45'E	
<b>Huerniopsis R. Br.</b>			
* <i>H. decipiens</i> N. E. Br.	22	R.S.A.: Northern Cape Prov., 11.4 km E Kuruman	Meve & Liede 580 [MSUN]
<b>Larryleachia Plowes</b>			
# <i>L. cactiformis</i> (Hook.) Bruyns	22	NAMIBIA: s. loc.	Albers 2513 [MSUN]
* <i>L. marlothii</i> (N. E. Br.) Bruyns	22	NAMIBIA: 8 km S Rosh Pinah	Albers & Meve 45 [MSUN]
* <i>L. picta</i> (N. E. Br.) Bruyns subsp. <i>picta</i>	22	NAMIBIA: ca. 29 km E Aus, Farm Plateau	Meve & Struck 178 [MSUN]
<b>Lavrania Plowes</b>			
<i>L. haagnerae</i> Plowes	22	NAMIBIA: 40–50 km SE Sesfontein, Khowarib Gorge	Haagner sub Plowes 5046 [PRE]
<b>Leptadenia R. Br.</b>			
<i>L. pyrotechnica</i> Decne.	22	EGYPT: 24 km W Safaga	Albers 3643 [MSUN]
<i>L. hastata</i> Decne.	22	GAMBIA: Abouko Natl. Park	S. Huber s.n.
<b>Neoschumannia Schltr.</b>			
<i>N. cardinea</i> (S. Moore) Meve	22	TANZANIA: E Usambara, Amani Forest Reserve	Meve & Liede 3359 [B, UBT]
* <i>N. kamerunensis</i> Schltr.	22	CAMEROON: Mt. Cameroon, NW Likombe	Meve & Etuge 910 [B, K, MSUN]



Taxon	2n	Locality	Voucher
<b>Notechidnopsis Lavranos &amp; Bleck</b>			
* <i>N. tessellata</i> (Pillans) Lavranos & Bleck	22	R.S.A.: Northern Cape Prov., ca. 13 km N Nieuwoudtville, "Uithoek"	Mere 255 [MSUN]
<b>Ophionella Bruyns</b>			
# <i>O. arcuata</i> (N. E. Br.) Bruyns subsp. <i>arcuata</i>	22	R.S.A.: Eastern Cape Prov.	Bruyns 4966 [MSUN, UBT]
<b>Orbea Haw.</b>			
<i>O. irroata</i> (Masson) L. C. Leach	22	s. loc.	s. coll.
# <i>O. longidens</i> (N. E. Br.) L. C. Leach	44	R.S.A.: Kwazulu-Natal, Lower Mt. Kergl	Hardy 6255
# <i>O. miscella</i> (N. E. Br.) Meve	22	R.S.A.: Eastern Cape Prov., Richmond	Bruyns 3237 [MSUN]
# <i>O. namaquensis</i> (N. E. Br.) L. C. Leach	22	R.S.A.: Northern Cape Prov., 4 km N Steinkopf	Albers & Meve 111 [MSUN]
<i>O. paradoxa</i> (Verd.) L. C. Leach	44	s. loc.	s. coll. [MSUN]
<i>O. rangeana</i> (Dinter & A. Berger) L. C. Leach	22	NAMIBIA: 1 km N Klein Karas	Albers 2356a [MSUN]
# <i>O. semota</i> (N. E. Br.) L. C. Leach	44	TANZANIA: s. loc.	Specks 921 [MSUN]
# <i>O. tapscottii</i> (Verd.) L. C. Leach	22	BOTSWANA: 15 km NW Molepolole	Plowes 7829
# <i>O. variegata</i> (L.) L. C. Leach	22	R.S.A.: Western Cape Prov., St. Helena Bay	Bruyns 4571 [MSUN]
# <i>O. variegata</i> (L.) L. C. Leach	44	R.S.A.: Eastern Cape Prov., Stytlerville	Albers 2466 [MSUN]
# <i>O. verrucosa</i> (N. E. Br.) L. C. Leach var. <i>verrucosa</i>	22	R.S.A.: Eastern Cape Prov., Grahamstown, Thomas Baines N. R. nr Damwall	Liede 2919 [MSUN]
<b>Orbeopsis L. C. Leach</b>			
# <i>O. albocastanea</i> (Marl.) L. C. Leach	22	NAMIBIA: s. loc.	Bruyns 3045
* <i>O. gerstneri</i> subsp. <i>elongata</i> (R. A. Dyer) L. C. Leach	22	R.S.A.: Mpumalanga, Pilgrim's Rest, Penge	Hardy 4095
<i>O. gerstneri</i> (Letty) L. C. Leach subsp. <i>gerstneri</i>	44	R.S.A.: Kwazulu-Natal, Empangeni	de Kock sub Albers 2551 [MSUN]
# <i>O. lutea</i> (N. E. Br.) L. C. Leach subsp. <i>lutea</i>	22	R.S.A.: Northern Cape Prov., 15 km W Potchefstroom	Albers 3525 [in hort. UBT]
# <i>O. lutea</i> (N. E. Br.) L. C. Leach subsp. <i>lutea</i>	22	ZIMBABWE: Bulawayo, Hyde Park	Albers, Liede & Meve 537 [MSUN]
# <i>O. melanantha</i> (Schltr.) L. C. Leach	44	ZIMBABWE: Zambezi Valley, between Deka River & Bin-ga River	Plowes 6502
<i>O. tsumebensis</i> (Oberm.) L. C. Leach	22	NAMIBIA: 5 km N Grootfontein	Rave s.n. [MSUN]
* <i>O. valida</i> (N. E. Br.) L. C. Leach	22	ZIMBABWE: Wankie Distr., Kamativi	Buckland s.n.
<b>Orthanthera Wight</b>			
# <i>O. albida</i> Schinz	22	NAMIBIA: near the Groot Welwitschia Vlakte	Albers 2727 [MSUN]
<b>Pachycymbium L. C. Leach</b>			
* <i>P. carnosum</i> (Stent) L. C. Leach	22	R.S.A.: Northern Cape Prov., Magaliesberg, Breeds Nek	Hardy sub Plowes 6715 [MSUN]



Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<b>Pectinaria Haw.</b>			
# <i>P. longipes</i> (N. E. Br.) Bruyns	22	R.S.A.: Western Cape Prov., Keetrom, Sutherland	Bruyns 2548 [MSUN]
<b>Piaranthus R. Br.</b>			
* <i>P. comptus</i> N. E. Br.	22	R.S.A.: Western Cape Prov., between Klaarstrom and Prince Albert	Albers et al. 10708 in K 1123 [MSUN]
* <i>P. decorus</i> (Masson) N. E. Br. subsp. <i>decorus</i>	22	R.S.A.: Western Cape Prov., near Sterkfontein	Bruyns 6290
* <i>P. parvulus</i> N. E. Br.	22	R.S.A.: Western Cape Prov., ca. 7 km SW Laingsburg (Witteberge)	Meve 288 [MSUN]
<b>Pseudolithos P. R. O. Bally</b>			
<i>P. caput-viperae</i> Lavranos	22	ex hort. Mesa Garden	s.n. [MSUN]
* <i>P. dodsonianus</i> (Lavranos) Bruyns & Meve	22	SOMALIA: 4 km NNW Erigavo	Lavranos 7326 [MSUN]
<b>Quaqua N. R. Br.</b>			
# <i>Q. acutiloba</i> (N. E. Br.) Bruyns	22	R.S.A.: Northern Cape Prov., 11 km N Concordia	Meve 213 [MSUN]
<i>Q. albersii</i> Plowes	22	R.S.A.: Western Cape Prov., bet. Vredendal and Holrivier to Liebendal	Albers 2252 [MSUN]
# <i>Q. cincla</i> (Lückh.) Bruyns	22	R.S.A.: Northern Cape Prov., N Concordia	Pehlemann 2737 [MSUN]
# <i>Q. incarnata</i> subsp. <i>aurea</i> (Lückh.) Bruyns	22	R.S.A.: Western Cape Prov., Pakhuis Pass	Albers 2031b [MSUN]
# <i>Q. incarnata</i> (L. f.) Bruyns subsp. <i>incarnata</i> var. <i>incarnata</i>	22	NAMIBIA: N Aus, branching off Helmeringhausen	Albers & Meve 95 [MSUN]
<i>Q. incarnata</i> subsp. <i>incarnata</i> var. <i>tentaculata</i> Bruyns	22	R.S.A.: Western Cape Prov., 40 km N Nieuwoudtville, Kerboomkop	Meve 246 [MSUN]
<i>Q. inversa</i> N. E. Br.	22	R.S.A.: Western Cape Prov., Bitterfontein	Bruyns 6133 [MSUN]
<i>Q. linearis</i> (N. E. Br.) Bruyns	22	R.S.A.: Western Cape Prov., Spreenfontein	Bruyns 2423 [MSUN]
# <i>Q. mammillaris</i> (L.) Bruyns	22	R.S.A.: Western Cape Prov., 15 km S VanRhynsdorp	Meve 146 [MSUN]
# <i>Q. marlothii</i> (N. E. Br.) Bruyns	22	R.S.A.: Western Cape Prov., 1 km N Karooport	Albers et al. K1415 [MSUN]
<i>Q. multiflora</i> N. E. Br.	22	R.S.A.: Northern Cape Prov., Calvinia	Bruyns 4297 [MSUN]
<i>Q. parviflora</i> (Masson) Bruyns subsp. <i>gracilis</i> (Lückh.) Bruyns	22	R.S.A.: Western Cape Prov., below Gannaga Pass	Bruyns 989 [MSUN]
<i>Q. parviflora</i> (Masson) Bruyns subsp. <i>pulchra</i> Bruyns	22	R.S.A.: Western Cape Prov., between Vredendal and Holrivier	Albers 2253
<i>Q. parviflora</i> (Masson) Bruyns subsp. <i>swanepoeltii</i> (Lavr.) Bruyns	22	R.S.A.: Northern Cape Prov., 30 km S Loerisfontein on road to Calvinia	Lavranos s.n. [MSUN]
<i>Q. pillansii</i> (N. E. Br.) Bruyns	22	R.S.A.: Western Cape Prov., Montagu, Kogmanskloof	EH 190 sub Albers 2553
<i>Q. pruinosa</i> (Masson) Bruyns	22	s. loc.	ex Kennedy sub Albers 2514 [MSUN]



## Appendix I. Continued.

Taxon	2n	Locality	Voucher
<i>Q. ramosa</i> (Masson) Bruyns	22	R.S.A.: Western Cape Prov., SW Laingsburg	Albers 2481 [MSUN]
<b>Rhytidocaulon P. R. O. Bally</b>			
<i>R. fulleri</i> Lavranos & Mort.	22	OMAN: Dhofar, 56 km E Salalah	Collenette 8439 [MSUN]
* <i>R. macrolobum</i> Lavranos subsp. <i>minimum</i> Meve & Collenette	22	SAUDI ARABIA: 60 km NW Najran	Collenette 8792 [MSUN]
<i>R. sheilae</i> D. V. Field	22	SAUDI ARABIA: Muhayl	Collenette 8964
<b>Riocreuxia Decne.</b>			
<i>R. burchellii</i> K. Schum.	22	R.S.A.: Kwazulu-Natal, s. loc.	ex hort. Shirley [MSUN]
<b>Stapelia L.</b>			
# <i>S. asterias</i> Masson	22	R.S.A.: Western Cape Prov., between Calitzdorp and Van- Wyksdorp	Albers et al. 10726 in K 1136 [MSUN]
<i>S. baylissii</i> L. C. Leach	22	R.S.A.: Eastern Cape Prov., Zuurberg Pass	Bayer s.n. [MSUN]
<i>S. erectiflora</i> subsp. <i>prostratiflora</i> L. C. Leach	22	R.S.A.: Western Cape Prov., Dornrivier Bridge	Bruyns 1289 [NBG]
# <i>S. gigantea</i> N. E. Br.	22	MALAWI: Lake Malawi	Albers 2575
<i>S. glanduliflora</i> Masson	22	R.S.A.: Western Cape Prov., 25 km S Klaver	Albers & Meve 04 [MSUN]
# <i>S. grandiflora</i> Masson	22	LESOTHO: NW Mafeteng, Hermon	Gerbaulet & Struck 23783 [MSUN]
# <i>S. hirsuta</i> L.	22	R.S.A.: Western Cape Prov., Veldrif	Albers 2498 [MSUN]
# <i>S. kwebensis</i> N. E. Br.	22	ZIMBABWE: Tuli, at Botswana border	Albers 2568 [MSUN]
<i>S. longipedicellata</i> (A. Berger) N. E. Br.	22	NAMIBIA: W Khorixas	Marschewski 114 [MSUN]
<i>S. montana</i> L. C. Leach var. <i>montana</i>	22	R.S.A.: Western Cape Prov., Groot Winterhoekberge, near Pardevlei	Bayer 1602 [MSUN, NBG]
# <i>S. pillansii</i> N. E. Br. var. <i>pillansii</i>	22	R.S.A.: Western Cape Prov., S. Palmietfontein, "Jager- skraal"	Meve 299
<i>S. remota</i> R. A. Dyer	22	NAMIBIA: Baynes Mtns. (Kaokaoveld)	Steenkamp sub Ploves 5146
# <i>S. rufa</i> Masson	22	R.S.A.: Western Cape Prov., 27 km S Laingsburg	Albers 2483 [MSUN]
<i>S. schinzii</i> A. Berger & Schltr. var. <i>schinzii</i>	22	NAMIBIA: W Windhoek	Pehlemann 445
<b>Stapelianthus Choux ex A. C. White &amp; B. Sloane</b>			
<i>S. arenarius</i> Bosser & Morat	22	MADAGASCAR: N Tuléar, Morombe road	Teissier 111 [MSUN]
<i>S. decaryi</i> Choux	22	MADAGASCAR: Beloha direction to Tsihomb, 4 km from Tsiomb	Liede, Conrad & Barad 2747 [MSUN]
<i>S. hardyi</i> Lavranos	22	MADAGASCAR: s. loc.	ex hort. de Boer [MSUN]
# <i>S. madagascariensis</i> (Choux) Choux	22	MADAGASCAR: Ambovombé direction to Antanimora, 15 km from Antanimora	Liede, Conrad & Barad 2788 [MSUN]



Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<i>S. montagnacii</i> (Boit.) Boit. & Bertrand	22	MADAGASCAR: s. loc.	s.n. [MSUN]
<i>S. pilosus</i> Lavranos & Hardy	22	MADAGASCAR: Amboasary (S)	Mies & Nober 51b
<b>Stapeliopsis Pill.</b> (= <i>Pectinaria</i> Haw. p.p.)			
<i>S. breviloba</i> (R. A. Dyer) Bruyns	22	s. loc.	ex hort. De Boer [MSUN]
# <i>S. exasperata</i> (Bruyns) Bruyns	22	R.S.A.: Northern Cape Prov., Middlepos, Wolvedans	Bruyns 4513 [MSUN]
# <i>S. pillansii</i> (N. E. Br.) Bruyns	22	R.S.A.: Eastern Cape Prov., Port Elizabeth, NW von Ann's Villa	Bruyns 1561
# <i>S. saxatilis</i> (N. E. Br.) Bruyns subsp. <i>saxatilis</i>	22	R.S.A.: Western Cape Prov., 19 km SE Oudtshoorn	Meve 410 [MSUN]
<b>Tavaresia Welw.</b>			
# <i>T. barklyi</i> (Dyer) N. E. Br.	22	NAMIBIA: Kaokoveld	Albers 3599 [MSUN]
<b>Tridentea Haw.</b>			
<i>T. duequensis</i> (Lückh.) L. C. Leach	22	R.S.A.: Northern Cape Prov., 45 km ESE Brandvlei	Karoo Garden 117/82 [MSUN]
# <i>T. gemmiflora</i> (Masson) Haw.	22	R.S.A.: Western Cape Prov., 13 km E Murraysburg	Meve 348 [MSUN]
# <i>T. jucunda</i> var. <i>cincta</i> (Marl.) L. C. Leach	22	R.S.A.: Eastern Cape Prov., 15 km S Hutchinson	Meve 349 [MSUN]
# <i>T. marientalensis</i> (Nel) Leach subsp. <i>albipilosa</i> (Gies) Leach	22	NAMIBIA: Karasburg, Farm Elandsdraai (WSW Ari-amsvlei)	Albers 2348 [MSUN]
# <i>T. pachyrrhiza</i> (Dinter) L. C. Leach	22	R.S.A.: Northern Cape Prov., Richtersveld, Oranjenmund	Hardy 4739
<i>T. parvipuncta</i> var. <i>truncata</i> (Lückh.) L. C. Leach	22	R.S.A.: Western Cape Prov., Botterkloof Pass	Vorster & Lavranos 2994 [MSUN]
<i>T. virescens</i> (N. E. Br.) L. C. Leach	22	R.S.A.: Northern Cape, N Brandvlei	Lamberti s.n. [in cult. UBT]
<b>Tromotriche Haw.</b>			
# <i>T. aperta</i> (Masson) Sweet	22	R.S.A.: Richtersveld	Visser sub Albers 2498 [MSUN]
# <i>T. baylissii</i> (L. C. Leach) Bruyns var. <i>baylissii</i>	22	R.S.A.: Eastern Cape Prov., Kouga Dam	v. Jaarsveld 11057 [MSUN]
# <i>T. choanantha</i> (Lavranos & Hall) Bruyns	22	R.S.A.: Eastern Cape Prov., Kleinberg	v. Jaarsveld 684/87 [MSUN]
# <i>T. longii</i> (Lückh.) Bruyns	22	R.S.A.: Eastern Cape Prov., 55 km SE Jansenville, Parde-poort	Albers 2464 [MSUN]
* <i>T. longipes</i> (Lückh.) Bruyns	22	NAMIBIA: ca. 16 km N Rosh Pinah	Albers & Meve 75 [MSUN]
# <i>T. revoluta</i> (Masson) Haw.	22+2B	R.S.A.: Western Cape Prov., 9 km S Botterkloof Pass	Albers 2048a [MSUN]
<i>T. ruschiana</i> (Dinter) Bruyns	22	s. loc.	cult. J. Thompson
<b>White-sloanea Chiov.</b>			
<i>W. crassa</i> (N. E. Br.) Chiov.	22	SOMALIA: between Garawe and Gardo, Dan Garayo	Lavranos & Barad s.n.



Taxon	2n	Locality	Voucher
<b>Tribe: ASCLEPIADEAE (R. Br.) Duby</b>			
<b>Subtribe: Asclepiadinae Endl. ex Meisn.</b>			
<b>Asclepias L.</b>			
# <i>A. fascicularis</i> Decne.	22	U.S.A.: ex hort. Davis	ex hort. Davis [UBT]
<i>A. flava</i> N. E. Br.	22	ARGENTINA: San Pedro de Colalao (Tucumán)	Liede 3096
# <i>A. linaria</i> Cav.	22	MEXICO: Michoacán, 3 km NW Los Reyes and 25 km E Maravatio	Conrad 9305 [MSUN]
<i>A. tuberosa</i> L.	22	U.S.A.: ex hort BG Michigan	ex hort. BG Michigan
<b>Calotropis R. Br.</b>			
<i>C. gigantea</i> (L.) R. Br.	22	TANZANIA: Amboni	Liede & Meve 3378 [UBT]
<i>C. procera</i> (Ait.) Ait. f.	22	KENYA: Rift Valley to Baringo, W Koriema	Liede & Newton 3177
<b>Gomphocarpus R. Br.</b>			
<i>G. cancellatus</i> (Burm. f.) Bruyns	22	R.S.A.: Western Cape Prov., Rooinekpass	Albers 3031 [MSUN]
<i>G. filiformis</i> (E. Mex.) Dieler	22	NAMIBIA: near Groot Welwitschia Vlakte	Albers 2726 [MSUN]
<i>G. linearis</i> D. Dieler	22	KENYA: Naivasha, Nakuru-Nairobi (Rift Valley)	Liede 3180 [ULM]
<i>G. tenuifolius</i> (N. E. Br.) Bullock	22	ZIMABAWE: Mtoko	Albers, Liede & Meve 511 [MSUN]
<b>Kanahia R. Br.</b>			
<i>K. laniflora</i> (Forssk.) R. Br. s.l.	22	KENYA: Teita, Sala Gate, (Tsavo East)	Liede & Newton 3211 [E, MSUN, ULM]
<i>K. laniflora</i> (Forssk.) R. Br. s. str.	22	YEMEN: North	Mangelsdorff Y116 [UBT]
<b>Pergularia L.</b>			
# <i>P. daemia</i> (Forssk.) Chiov. var. <i>daemia</i>	22	CAMEROON: Rhumsiki, centre of village	Mere 920 [MSUN]
# <i>P. daemia</i> (Forssk.) Chiov. var. <i>daemia</i>	22	TANZANIA: Moshi, Rau-Forest	Liede & Meve 3367 [UBT]
<i>P. daemia</i> (Forssk.) Chiov. var. <i>macrantha</i> Chiov.	22	KENYA: 56 km W Malindi	Liede & Newton 3209 [ULM]
<i>P. gariensis</i> N. E. Br.	22	R.S.A.: Northern Cape Prov., Richtersveld	Albers 3579 [MSUN]
<i>P. tomentosa</i> L.	22	YEMEN: 10 km W Madinet as Sharq	Mangelsdorff Y213 [UBT]
<b>Stathmostelma K. Schum.</b>			
<i>S. diversifolia</i> Goyder	22	KENYA: Narok, ca. 32.2 km on Kikorok Road, Loita Plains	Liede & Newton 3221 [K]
<b>Stenostelma Schltr.</b>			
<i>S. capense</i> Schltr.	22	R.S.A.: Eastern Cape Prov., Teviot Stn.	Liede 2934 [K, MSUN]



Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<b>Subtribe: Astephaninae Endl. ex Meisn.</b>			
<b>Microlooma R. Br.</b>			
* <i>M. incanum</i> Decne.	20	NAMIBIA: 5 km N Aus	Albers & Meve 88 [MSUN]
* <i>M. sagittatum</i> (L.) R. Br.	20	R.S.A.: Western Cape Prov., 22 km N Matjiesfontein	Meve 376a
* <i>M. tenuifolium</i> (L.) K. Schum.	20	R.S.A.: Western Cape, Kapokberg	Meve & Liede 623 [MSUN]
<b>Subtribe: Glossonematinae K. Schum.</b>			
<b>Glossonema Decne.</b>			
<i>G. boveanum</i> (Decne.) Decne. ssp. <i>boveanum</i>	22	KENYA: ca. 30 km from Loyengalami	Liede & Newton 3239 [UBT, ULM]
<b>Pentarrhinum E. Mey.</b>			
# <i>P. insipidum</i> E. Mey.	22	R.S.A.: Gauteng, Irene-Verwoerdburg	Liede 2941 [MSUN]
<i>P. insipidum</i> E. Mey.	24	KENYA: Isiolo	Liede & Newton 3225
<b>Subtribe: Gonolobinae (G. Don) Liede</b>			
<b>Fischeria DC.</b>			
<i>F. sp.</i>	22	COSTA RICA: Region Guana Caste, Cabo Blanco	Voigt s.n. [in cult. UBT]
<b>Gonolobus Michx.</b>			
<i>G. barbatus</i> HBK	22	MEXICO: Jalisco, 2 km NE Tequila	Conrad 9325 [UBT]
<b>Macrocephis Kunth</b>			
<i>M.sp. (near urceolata Karst.)</i>	22	GUATEMALA: 60 km N Guatemala-City	Heyne s.n. [UBT]
<b>Matelea Aubl.</b>			
<i>M. carolinensis</i> (Jacq.) R. E. Woodson	22	U.S.A.: Georgia, Athens	Lipow s.n.
<i>M. cyclophylla</i> (Standl.) R. E. Woodson	22	MEXICO: s. loc.	ex hort. G. Barad
<b>Subtribe: Metastelminae Endl. ex Meisn.</b>			
<b>Blepharodon Decne.</b>			
<i>B. salicinum</i> Decne.	22	ECUADOR: betw. Estación Científica San Francisco and Zamora	Liede 3304 [ULM]
<b>Cynanchum L.</b>			
<i>C. abyssinicum</i> Decne.	22	TANZANIA: Arusha Prov., Olmoti Crater	Liede & Meve 3373 [UBT]
<i>C. ampanihense</i> Jum. & H. Perrier	22	MADAGASCAR: Cap St. Marie	Liede 2817a [MSUN]
<i>C. andringitrense</i> Choux	22	MADAGASCAR: s. loc.	Rauh s.n. [MSUN]
<i>C. angavokeliense</i> Choux	22	MADAGASCAR: s. loc.	s.n. ex Specks [MSUN]



## Appendix I. Continued.

Taxon	2n	Locality	Voucher
<i>C. appendiculatopsis</i> Liede	22	MADAGASCAR: s. loc.	Fervier s.n. [MSUN]
<i>C. arenarium</i> Jum. & H. Perrier	22	MADAGASCAR: Tuléar, 15 km to Antanimora	Liede 2789
<i>C. auriculatum</i> Royle ex Wight	22	BHUTAN: Pass from Thimpu to Wangduephodrang	Liede 3281 [MSUN]
<i>C. bisinuatum</i> Jum. & H. Perrier	22	MADAGASCAR: Toliara	Descoings 28283 [UBT]
<i>C. boerhaviifolium</i> Hook. & Arn.	22	CHILE: ca. 2 km N Los Vilos	Liede 3062
<i>C. compactum</i> Rauh	22	MADAGASCAR: Fianarantsoa, ca. 42 km W Ambatofinadrahana	Supthut & v. Arx 3029
<i>C. cucullatum</i> N. E. Br.	22	MADAGASCAR: Ankaratra	Liede 2868 [MSUN]
<i>C. descoingsii</i> Rauh	22	MADAGASCAR: Tuléar	Descoings 28244
<i>C. erythranthum</i> Jum. & H. Perrier	22	MADAGASCAR: Ankarana	Mangelsdorff M 26
<i>C. danguyanum</i> Choux	22	MADAGASCAR: Maintirano	Mangelsdorff 44 [UBT]
<i>C. formosum</i> N. E. Br.	22	CHILE: Los Vilos, ca. 2 km from town	Liede & Conrad 3061 [MSUN, UBT]
# <i>C. gerrardii</i> (Harv.) Liede	22	KENYA: 30 km N Maralal	Meve 962 [MSUN]
<i>C. gerrardii</i> (Harv.) Liede	22	MADAGASCAR: betw. Ambovombé and Antanimora, side-track to Angavo	Liede 2797 [MSUN]
# <i>C. hardyi</i> Liede & Meve	22	MADAGASCAR: Ankarafansika	Mangelsdorff M37
<i>C. implicatum</i> Jum. & H. Perrier	22	MADAGASCAR: Montagne des Francais	Mangelsdorff 24
<i>C. juliani-marnieri</i> Descoings	22	MADAGASCAR: Cap St. Marie	ex hort. Les Cèdres [MSUN]
<i>C. laeve</i> Pers.	22	U.S.A.: Missouri, St. Louis, near Shaw Arboretum	Liede s.n. [UBT]
<i>C. lecomtei</i> Choux	22	MADAGASCAR: Cap St. Marie	Liede 2817b [MSUN]
<i>C. leucanthum</i> K. Schum. subsp. <i>elongatum</i> Liede	22	MADAGASCAR: 48 km W Samabava	Mangelsdorff 410 [UBT]
<i>C. madagascariense</i> K. Schum.	22	MADAGASCAR: forest 43 km from Ft. Dauphin	Liede 2756 [MSUN]
<i>C. marnieranum</i> Rauh	22	MADAGASCAR: 43 km from Ambovombé direction to Tsi-hombé	Liede 2805 [MSUN]
<i>C. messeri</i> (Buchenau) Jum. & H. Perrier	22	MADAGASCAR: between Beloha and Ampanihy, 5 km from Beloha	Liede 2831
# <i>C. metei</i> Liede	22	MADAGASCAR: Tuléar, S de la Table	Teissier 214 [MSUN]
<i>C. montevidensis</i> Spreng.	22	ARGENTINA: Chaco, Isla del Cerrito	Liede & Conrad 3019a [ULM]
<i>C. nodosum</i> (Jum. & H. Perrier) Descoings	22	MADAGASCAR: 15 km from Antanimora to Ambovombé	Liede 2789
<i>C. nummulariifolium</i> Hook & Arn.	22	ARGENTINA: Las Lenas, Valle de las Moches	Liede 3050 [ULM]
<i>C. obovatum</i> (Decne.) Choux	22	MADAGASCAR: ca. 7 km from Ambalamanakana (to Am-bosita)	Liede 2866 [MSUN]
# <i>C. obtusifolium</i> L. f.	22	R.S.A.: Eastern Cape Prov., Misfor	Liede 2925 [UBT]
<i>C. ovalifolium</i> Wight	22	AUSTRALIA: ca. 1.5 km upstream Brown crossing, rd. to Lockhart River Misn.	Forster 4090



Appendix 1. Continued.

Taxon	2n	Locality	Voucher
<i>C. papillatum</i> Choux	22	MADAGASCAR: Andringitra	Liede & Conrad 2862 [MSUN]
<i>C. perrieri</i> Choux	22	MADAGASCAR: s. loc.	Descoings 28283
# <i>C. petignatii</i> Liede & Rauh	22	MADAGASCAR: Tuléar	Teissier 269 [UBT]
<i>C. philipponianum</i> Liede & Meve	22	MADAGASCAR: Ankarana, Tsingy	Mangelsdorff M 25 [MSUN]
<i>C. rauhianum</i> Descoings	22	MADAGASCAR: Isalo	Röösli s.n.
<i>C. repandum</i> Decne.	22	MADAGASCAR: Ankaratra	Liede 2867 [MSUN]
<i>C. rossii</i> Rauh	22	MADAGASCAR: Cap St. Marie	Singer 072478 [MSUN, ZSS]
<i>C. serpyllifolium</i> Kunth	22	ECUADOR: Carachi, El Angel-Tulcan road at Pico Aquero	Bremer et al. 3372 [MSUN, UPS]
<i>C. sessiliflorum</i> (Decne.) Liede	22	MADAGASCAR: 15 km from Windsor Castle	Mangelsdorff 13 [MSUN]
<b>Folotsia Costantin &amp; Bois</b>			
<i>F. grandiflora</i> Jum. & H. Perrier	22	MADAGASCAR: Ambovombé to Antanimora, km 24 on sidetrack to Angavo	Liede 2796 [ULM]
<b>Funastrum E. Fourn.</b>			
<i>F. angustissimum</i> (Anderss.) E. Fourn.	20	ECUADOR: Galapagos Islands, s. loc.	Stevens s.n.
<i>F. arenarium</i> (Decne. ex Benth.) Liede	20	MEXICO: San Carlos, road to Beach (Baja California)	Liede & Conrad 2951 [MSUN, ULM]
<i>F. bilobum</i> (Hook. & Arn.) Macbride	20	MEXICO: Chiapas, La Trinitaria	Stevens 25744
<i>F. clausum</i> (Jacq.) Schultes	20	U.S.A.: Florida, Everglades, Reclamation site John Strekl Park	Liede 3000
<i>F. crispum</i> (Benth.) Schltr.	44	U.S.A.: Texas, Hueco Tanks State Park	Liede & Meve 2504 [MO]
# <i>F. cynanchoides</i> (Decne.) Schltr. subsp. <i>cynanchoides</i>	20	MEXICO: Todos Santos, Sierra Laguna trail (Baja California)	Liede & Conrad 2958
<i>F. odoratum</i> (Hemsl.) Schltr.	20	GUATEMALA: Guatemala City, Mixto, Fritz Richter's House	Liede 3244 [UBT]
<b>Grisebachiella Lorentz</b>			
<i>G. hieronymi</i> Lorentz	20	ARGENTINA: 3 km to Las Moches from Las Lenas (Mendoza)	Liede & Conrad 3053 [MSUN, ULM]
<b>Karimbolea Desc.</b>			
# <i>K. macrantha</i> (Jum. & H. Perrier) Liede & Meve	22	MADAGASCAR: Cap Ste. Marie, 150–200 m from light-house along road	Liede 2829
<b>Metaplexis R. Br.</b>			
# <i>M. japonica</i> (Thunb.) Makino	22, 24	RUSSIA: Primorsk Region	ex hort. Tartu [UBT, ULM]
<b>Metastelma R. Br.</b>			
<i>M. parviflorum</i> R. Br.	22	VENEZUELA: Tocopéro	Liede & Meve 3329 [ULM]



Taxon	2n	Locality	Voucher
<b>Orthosia Decne.</b>			
<i>O. rubens</i> (L. Wms.) Liede ined.	20	MEXICO: Los Azufres, ± 15 km NW of Ciudad Hidalgo	Conrad 9396 [MSUN, UBT]
<i>O. sp.</i>	20	ECUADOR: Quito	Liede & Meve 3473 [UBT]
<b>Oxystelma R. Br.</b>			
<i>O. bornouense</i> R. Br.	22	KENYA: Coast, ex hort.	Liede & Newton 3202 [ULM]
<i>O. esculentum</i> R. Br.	22	EGYPT: Elephantine Island	Shirley s.n.
<b>Pentacypus Schltr.</b>			
<i>P. lehmannii</i> (Schltr.) Liede	22	ECUADOR: Loja, Yananga	Liede 3333 [UBT]
<b>Philibertia Knuth</b>			
* <i>P. gilliesii</i> Lillo	18	ARGENTINA: Mendoza, La Crucecita, ca. 1.5 km from intersection	Liede 3054 [MSUN]
<i>P. gilliesii</i> Lillo	20	ARGENTINA: Jujuy, Laguna de Yala	Liede 3111
<i>P. lysimachioides</i> (Wedd.) T. Meyer	20	BOLIVIA: La Paz, Copacabana peninsula, 8 km from San Pedro	Liede 3139 [MSUN]
<b>Platykeleba N. E. Br.</b>			
<i>P. insignis</i> N. E. Br.	22	MADAGASCAR: Antanarivo	Rauh 68500
<b>Sarcostenma R. Br.</b>			
# <i>S. acidum</i> (Roxb.) Voigt	22	NEPAL: NE Dharapani, near Bheri River	Bruyns s.n.
# <i>S. antstranense</i> Meve & Liede	22	MADAGASCAR: 75 km N Sambava	Mangelsdorff 47 [UBT]
# <i>S. arabicum</i> Bruyns & P. I. Forst.	22	YEMEN: SW Sana'a	Radcliffe-Smith 4624 [K]
<i>S. brevipedicellatum</i> P. I. Forst.	22	AUSTRALIA: Gregory North Distr. (Qld.), 86 km from Winton on Boulia Road	Forster 5876
* <i>S. forskaolianum</i> Schult.	22	YEMEN: 78 km S Dhamar, near branching off Zulmah on Sumarah-Ibb Road	Noltee 864
# <i>S. pearsonii</i> N. E. Br.	22	R.S.A.: Northern Cape Prov., Smorenskadu	Liede 2523 [MSUN]
<i>S. resiliens</i> B. R. Adams & R. W. K. Holland	22	ZIMBABWE: 15 km NNW of Rusape	Albers, Liede & Meve 515 [MSUN]
# <i>S. stoloniferum</i> Adams & Holland	44	KENYA: Rumuruti, Kisima Ranch	Liede & Newton 3174 [MSUN]
<i>S. viminalis</i> (L.) R. Br. subsp. <i>australe</i> (R. Br.) P. I. Forst.	22	AUSTRALIA: Telowie Gorge (SA)	Meve & Hellbrugge 723 [MSUN]
<i>S. viminalis</i> subsp. <i>brunonianum</i> (Wight & Arn.) P. I. Forst.	22	AUSTRALIA: S Kennedy Distr. (Qld.), Thomas Is., NW shore	Bolton 700 [MSUN]
<i>S. viminalis</i> subsp. <i>brunonianum</i> (Wight & Arn.) P. I. Forst.	22	YEMEN: Suq As Sabt, Jabal Bura	Wood 3431 [K]



Appendix I. Continued.

Taxon	2n	Locality	Voucher
# <i>S. viminalis</i> subsp. <i>odontolepis</i> (Balf. f.) Meve & Liede	22	KENYA: Kilifi, Arabuko, Sokoke forest	Field & Powys 186 [MSUN]
* <i>S. viminalis</i> subsp. <i>orangeanum</i> Meve & Liede	22	NAMIBIA: Steinhausen, S Gobabis	Meve & Liede 599 [MSUN]
* <i>S. viminalis</i> subsp. <i>thunbergii</i> (Don) Liede & Meve	44	R.S.A.: Western Cape Prov., Atties, 1.5 km S Wiedow's River	Liede & Hammer 2507
# <i>S. viminalis</i> subsp. <i>stipitaceum</i> (Forssk.) Meve & Liede	22	YEMEN: 1 km E Al Barh	Noltee 233 [MSUN]
# <i>S. viminalis</i> (L.) R. Br. subsp. <i>viminalis</i>	22	MADAGASCAR: between Ampanihy and Androka, 73 km from Ampanihy	Liede 2701
<b>Schizostephanus Hochst. ex Benth. &amp; Hook. f.</b> <i>S. alatus</i> Hochst. ex K. Schum.	22	KENYA: Kilifi, Chasimba Hills	Keneally 9478
<b>Subtribe: Oxypetalinae K. Schum.</b> <b>Amblystigma Benth.</b> <i>A. cionophorum</i> Fourn.	22	ARGENTINA: Yerba Buena (Tucumán)	Liede 3069
<b>Araujia Brot.</b> <i>A. angustifolia</i> Steud.	20	ARGENTINA: Hurlingham, English Club	Liede 3014 [UBT, ULM]
<i>A. hortorum</i> E. Fourn.	22	ARGENTINA: Buenos Aires, Avenida San Martin	Liede 3010
<i>T. brunonis</i> Hook. & Arn.	40	ARGENTINA: Mendoza, Godoy Cruz	Liede 3058 [ULM]
<b>Morrenia Lindl.</b> <i>M. odorata</i> Lindl.	22	ARGENTINA: Chaco, Resistencia	Liede 3020 [ULM]
<b>Oxypetalum R. Br.</b> <i>O. balsanae</i> Malme	18	ARGENTINA: Mendoza, Campground "El Challosa"	Liede & Conrad 3059 [MSUN]
<i>O. coeruleum</i> (D. Don) Decne.	28	ARGENTINA: s. loc.	ex hort. [MSUN]
<i>O. ostenii</i> Malme	22	ARGENTINA: Iguacu, Sendero Macuru	Liede 3042 [MSUN]
<i>O. solanoides</i> Hook. & Arn.	18	ARGENTINA: Buenos Aires, I.N.T.A. area	Liede & Conrad 3011 [ULM]
<b>Tweedia Hook. &amp; Arn.</b> <i>T. brunonis</i> Hook. & Arn.	40	ARGENTINA: Mendoza, Godoy Cruz la Ripiera	Liede & Conrad 3058 [UBT, ULM]
<b>Subtribe: Tylophorinae (K. Schum.) Liede</b> <b>Blyttia Arn.</b> <i>B. fruticulosa</i> (Decne.) D. V. Field	22	KENYA: A.I.C. Chemolingot Bore Hole	Liede 2946 [MSUN]
<b>Diplostigma K. Schum.</b> <i>D. canescens</i> K. Schum.	22	TANZANIA: S Pare Mts., NE Mkomazi	Liede & Meve 3388 [UBT]



## Appendix I. Continued.

Taxon	2n	Locality	Voucher
<b><i>Pentatropis</i> R. Br. ex Wight &amp; Arn.</b>			
<i>P. madagascariensis</i> Decne.	22	MADAGASCAR: 4 km from Tsiomb, between Beloha and Tsihomb	Liede 2749 [P, UBT]
<i>P. nivalis</i> (J. F. Gmel.) D. V. Field & J. F. Wood	22	KENYA: near Hell's Kitchen	Meye 949 [MSUN, UBT]
<b><i>Pleurostelma</i> K. Schum.</b>			
<i>P. cernuum</i> (Decne.) Bullock	22	TANZANIA: W Tanga	Liede & Meye 3377 [UBT]
<b><i>Tylophora</i> R. Br.</b>			
<i>T. apiculata</i> K. Schum.	22	KENYA: Tana River Distr. Hewani Forest	Robertson & Guffa 6894 [MSUN]
<i>T. barbata</i> R. Br.	22	AUSTRALIA: 2 km S Kioloa (NSW)	Meye & Hellbrügge 790 [MSUN]
<i>T. coriacea</i> Marais	44	MAURITIUS: Isle Rinde	Bernadi s.n. [BR, UBT]
<i>T. flexuosa</i> R. Br.	22	PHILIPPINES: Laguna/Quezon, ascent to Mt. Banahaw	Schneidt & Liede 96-31 [K, ULM]
<i>T. heterophylla</i> N. E. Br.	22	KENYA: Naivasha, Aberdares, 5 km before junction	Liede 3155 [MSUN, ULM]
<i>T. hirsuta</i> (Burm. f.) Merr.	22	INDIA: Allahabad	Chaturvedi s.n. [MSUN]
# <i>T. indica</i> (M. Burm.) Merr.	22	INDIA: s. loc.	Bruyns s.n. [MSUN]
<i>T. oblonga</i> N. E. Br.	22	CAMEROON: Mt. Cameroon, NW Likombe	Meye 915 [B, MSUN]
<i>T. perrottetiana</i> Decne.	22	PHILIPPINES: Los Banos, IRR1-Ground	Liede 3252 [MSUN]
<i>T. tenuipedunculata</i> K. Schum.	22	KENYA: Arabuko Sokoke Forest	Liede 3200 [MSUN]
<i>T. villosa</i> Blume	22	PHILIPPINES: Luzon, Alaminos	Schneidt & Liede 96-109 [AUH]
<b><i>Vincetoxicum</i> Wolf</b>			
# <i>V. hirundinaria</i> Medik. ssp. <i>hirundinaria</i>	22	F.R.G.: Thüringen, Kyffhäuser-Mountains	Albers 3646 [MSUN]



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SUBTRIBE ASTEPHANINAE  
(APOCYNACEAE–  
ASCLEPIADOIDEAE)  
RECONSIDERED: NEW  
EVIDENCE BASED ON cpDNA  
SPACERS<sup>1</sup>

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Sigrid Liede<sup>2</sup>

ABSTRACT

The circumscription of the subtribe Astephaninae has a complex and convoluted history due in part to a scarcity of readily observed distinctive morphological characters. In this study the subtribe Astephaninae, as hitherto defined by morphological characters, is reexamined using sequences of the *trnT-L* and *trnL-F* spacer, as well as the *trnL* intron for 12 of its 15 genera. *Eustegia* is found to occupy an isolated basal position in the tribe Asclepiadeae, and *Schizostephanus* is transferred to the Metastelminae. The remaining 10 genera fall into two only distantly related clades of 3 and 7 genera, respectively. The Astephaninae s. str. comprise only 3 South African genera, *Astephanus* s. str., *Microloma*, and *Oncinema*. The other 7 genera form a well-supported clade, the subtribe Tylophorinae. Both groups comprise only Old World genera. All New World taxa studied, even those that have never been formally excluded from *Astephanus*, are found in a distinct, well-supported New World Metastelminae clade. Based on the results presented here one of the key characters of the asclepiads—the corona—has been lost independently at least twice: once in the south African Astephaninae, and once in the New World Metastelminae. This once again underscores the extreme lability of this morphologically complex organ, as well as the difficulties in assessing homology in the asclepiads. A corollary classification of the Asclepiadeae is provided as an Appendix.

*Key words:* Apocynaceae–Asclepiadoideae, Astephaninae, *trnL* intron, *trnT-L* and *trnL-F* spacer.

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The tribe Asclepiadeae, morphologically characterized by pendent pollinia and the possession of true styles (Swarupanandan et al., 1996), forms a monophyletic group occupying an advanced position in the Apocynaceae s.l. according to recent molecular studies (Sennblad, 1997; Civeyrel et al., 1998). The relationships among the ca. 100 Asclepiadeae genera, however, are much less clear. Schumann (1895) distinguished five subtribes using exclusively corona characters. In an attempt to define subtribes on a broader range of apomorphic characters Liede (1997) also recognized five groups, but with a largely different composition. As a sixth subtribe, she added the Gonolobinae following Swarupanandan et al. (1996).

The subtribe Astephaninae Endl. ex Meisn. (1840) originally contained only three genera: *Astephanus* R. Br., *Haemax* E. Mey. (a synonym of *Astephanus*), and *Hybanthera* Endl. (a synonym of *Tylophora* R. Br.). Schumann (1895) considered the subtribe to comprise nine genera: *Microloma* R. Br. from southern Africa, *Adelostemma* Hook. f., and

*Henrya* Hemsl. (another synonym of *Tylophora*) from Asia, as well as *Amblystigma* Benth., *Esmeraldia* E. Fourn. (a synonym of *Metastelma* R. Br.), *Hemipogon* Decne., *Mitostigma* Decne., and *Nautonia* Decne. all from South America. *Astephanus*, founded by Brown (1810) exclusively on southern African material and regarded by him as a close relative of *Microloma* (Brown, 1810), was soon extended to contain American taxa without a corona. However, since the absence of a feature—in this case the corona—is not meaningful as an indication of relationship, both the circumscription of the subtribe Astephaninae and of the genus *Astephanus* were in need of reexamination.

Most experts now agree that *Astephanus* s. str. is restricted to the Old World and comprises only three species (*A. marginatus* Schltr., *A. neglectus* Schltr., and *A. triflorus* R. Br.) as stated in Liede (1994). Most of the New World members formerly included in the genus *Astephanus* have been interpreted meanwhile as species with a reduced corona within various currently recognized genera with

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